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Evaluating Forecasting Procedures for Predicting Pacific Herring (*Clupea harengus pallasi*) Recruitment in British Columbia

M. Stocker and D. J. Noakes

Department of Fisheries and Oceans, Biological Sciences Branch, Pacific Biological Station, Nanaimo, B.C. V9R 5K6

Stocker, M., and D. J. Noakes. 1988. Evaluating forecasting procedures for predicting Pacific herring (*Clupea harengus pallasi*) recruitment in British Columbia. Can. J. Fish. Aquat. Sci. 45: 928–935.

The ability of four forecasting methods to generate one-step-ahead forecasts of Pacific herring (*Clupea harengus pallasi*) recruitment is considered in this paper. Recruitment time series for five coastal stocks and various environmental time series are employed in the analyses. Information up to and including time t is employed to estimate the parameters of each model used to forecast recruitment in year $t + 1$. Parameter estimates are then updated after each time step with a total of seven one-step-ahead forecasts being generated by each model for each stock. The forecast errors are compared using the five criteria: (1) root mean squared error, (2) mean absolute deviation, (3) mean absolute percent error, (4) median absolute deviation, and (5) median absolute percent error. The results of the study indicate that time series models may provide better forecasts of recruitment for the Strait of Georgia/Johnstone Strait stocks than the other competing procedures. A Ricker stock–recruitment model that takes into account environmental data appears to produce marginally better forecasts for the Central Coast and Queen Charlotte Island stocks, while all models produced equally good/bad forecasts for the Prince Rupert district stocks.

On examine dans cet article la capacité de quatre méthodes de fournir des prévisions par intervalle de temps du recrutement de harengs du Pacifique (*Clupea harengus pallasi*). On utilise pour les analyses des séries chronologiques du recrutement pour cinq stocks côtiers et diverses séries chronologiques environnementales. On se sert des informations jusqu'au temps t inclusivement pour estimer les paramètres de chaque modèle employé pour prédir le recrutement au cours de l'année $t + 1$. Les estimations des paramètres sont ensuite mises à jour après chaque intervalle de temps, sept prévisions au total étant fournies par chaque modèle pour chaque stock. On compare les erreurs de prévision en se servant des cinq critères suivants : 1) erreur de la moyenne quadratique, 2) écart absolu moyen, 3) erreur absolue en pourcentage de la moyenne, 4) écart absolu de la médiane et 5) erreur absolue en pourcentage de la médiane. Les résultats de l'étude montrent que les modèles de séries chronologiques peuvent fournir de meilleures prévisions du recrutement pour les stocks du détroit de Géorgie et du détroit de Johnstone que les autres méthodes concurrentes. Un modèle de stock–recrutement de Ricker qui tient compte des données environnementales semble produire des prévisions légèrement supérieures pour les stocks de la côte centrale et des îles de la Reine-Charlotte tandis que tous les modèles ont donné des prévisions tout aussi bonnes ou mauvaises pour les stocks du district de Prince Rupert.

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Forecasting the size of year-classes recruiting to a fishery is of fundamental importance in fisheries management. This assertion holds particularly true in high turnover, fast growing pelagic species such as Pacific herring (*Clupea harengus pallasi*). For these species, new recruits can represent a considerable (>20%) proportion of the total stock biomass and may significantly influence quotas established by fisheries managers.

Stock–recruitment models (e.g. Ricker 1954; Beverton and Holt 1957; Cushing 1973) are frequently used to forecast year-class strength. These models forecast recruitment from stock size using a functional relationship, and they always exhibit a wide range of variability around the average relationship (e.g. Garrod and Jones 1974; Rothschild and Mullen 1985; Smith and Walters 1981; Stocker et al. 1985). The time series approach to modelling stock and recruitment is an alternative approach making use of the inherent autocorrelation structure of both the recruitment and stock time series (Noakes et al. 1987).

In this paper we evaluate the performance of the two categories of models for forecasting year-class strength. We begin with a discussion of model types, define the evaluation criteria in the form of error measurements, and examine four models for forecasting year-class strength for five herring stocks on the British Columbia coast.

Methods

Data Sources

The main data sources for this study include (1) estimates of Pacific herring year-class strength, (2) spawn indices, and (3) environmental data. Herring data are collected by season starting July 1 and ending June 30. A cohort is dated by season as fish in their first year of life. For example, spawn for the 1950–51 season (t) is deposited in March of 1951 producing the 1951 cohort of the 1951–52 season ($t + 1$). The data series used in this study includes the period 1950–82.

Recruitment estimates (measured as $N_{t+1,1}$) for five stock groupings on the British Columbia coast (Haist et al. 1985) were derived from stock reconstructions using an age-structured model (Fournier and Archibald 1982). The spawn index in season *t* is the sum of spawn length times width times intensity for each of the five stock groupings (Haist et al. 1985). Environmental variables analysed include monthly means of sea surface temperature (SST), sea level (SLEV), salinity (SAL), river discharge (FRASER), and Ekman transport (TRANS).

Forecasting Methods

We use four methods to forecast year-class strength ($N_{t+1,1}$). Two methods employ stock–recruitment models, whereas the other two methods rely on time series analysis.

Ricker stock–recruitment models

Ricker (1954) related recruitment to stock abundance:

$$(1) \quad N_{t+1,1} = \alpha \cdot S_t \cdot \exp(-\beta \cdot S_t)$$

where $N_{t+1,1}$ is recruitment at the beginning of season $t + 1$, S_t is spawning stock index in season *t*, α is the density-independent parameter, and β is the density-dependent parameter and specifies the replacement spawning abundance. Maximum likelihood estimates of α and β are used in the above relationship (equation (1)) to forecast year-class strengths.

A modified version of the Ricker stock–recruitment model is derived when we assume that deviations from predicted recruitment are attributable to changes in the α parameter over time. In this model, α is considered to be a function of environmental conditions (Tang 1985):

$$(2) \quad \alpha_t' = g[x_{1t}, x_{2t}, \ldots, x_{mt}]$$

where x_{it} is an environmental factor in spawning season *t* such as SST and α_t' is an index of environmental conditions affecting density-independent mortality in season *t*. Substituting (2) into (1) yields our second method used for forecasting herring year-class strengths:

$$(3) \quad N_{t+1,1} = g[x_{1t}, x_{2t}, \ldots, x_{mt}] \cdot S_t \cdot \exp(-\beta \cdot S_t).$$

To select significant environmental factors for inclusion in (3), we used the technique of "exploratory correlation" (Ricker 1975; Stocker et al. 1985). The recruitment estimates ($N_{t+1,1}$) were correlated with monthly means of environmental factors thought important in the early life history of Pacific herring.

Parameter estimates were obtained employing the two-stage procedure outlined by Tang (1985). In the first stage, estimates of α and β were calculated using equation (1). Parameter β was considered to be a characteristic of the stock and not a function of time, while α represents an average of the α_t's in (2). The estimated β was used to calculate α_t's such that

$$(4) \quad \alpha_t = \frac{N_{t+1,1}}{S_t} \cdot \exp(\beta S_t).$$

The α_t's calculated in (4) were then employed in the second stage of the estimation procedure to establish the link with various environmental variables. The relationship between α_t and the environmental factors was assumed to be linear such that

$$(5) \quad \alpha_t = a_0 + \sum_{i=1}^{m} a_i \cdot x_{it}.$$

The parameters a_0 and a_i were estimated by multiple linear regression. Given a time series of $N_{t+1,1}$, S_t and x_{it}, and estimates of a_0, a_i, and β, year-class strengths were forecast using equation (3).

TABLE 1. Assumptions employed to formulate the general transfer function noise model as the Ricker and Cushing stock–recruitment functions.

Ricker	Cushing
$y_t = \ln N_{t+1,1}$	$y_t = \ln N_{t+1,1}$
$x_{1t} = S_t$	$x_{1t} = \ln S_t$
$x_{2t} = \ln S_t$	$x_{2t} = 1$ (for all t)
$x_{3t} = 1$ (for all t)	$b_i = k^a$
$b_i = k^a$	$\omega_1(B)\{\delta_1(B)\}^{-1} = -\beta$
$\omega_1(B)\{\delta_1(B)\}^{-1} = -\beta$	$\omega_2(B)\{\delta_2(B)\}^{-1} = \ln \alpha$
$\omega_2(B)\{\delta_2(B)\}^{-1} = 1$	$\theta(B)\{\phi(B)\}^{-1} = 1$
$\omega_3(B)\{\delta_3(B)\}^{-1} = \ln \alpha$	
$\theta(B)\{\phi(B)\}^{-1} = 1$	

[a] k = recruitment lag.

Time series models

The stock–recruitment models discussed above have a structure based on biological assumptions. An alternative form of forecasting is time series analysis. We use a single method which assumes no serial correlation of recruitment. The running average recruitment $\bar{N}_1$ is used to forecast $N_{t+1,1}$:

$$(6) \quad \bar{N}_1 = \frac{N_{1,1} + N_{2,1} + \ldots + N_{n,1}}{n}$$

where *n* observations are available in the time series.

A time series approach to stock–recruitment analysis has been proposed by Noakes et al. (1987). In their paper, these authors employed a transfer function noise (TFN) model (Box and Jenkins 1970) to examine the relationship between spawning stock size and subsequent recruitment. The general TFN model used is given by

$$(7) \quad (y_t - \mu_y) = \sum_{i=1}^{m} \omega_i(B)\{\delta_i(B)\}^{-1} B^{b_i}(x_{it} - \mu_{xi}) + \theta(\mathrm{B})\{\phi(B)\}^{-1} a_t$$

where y_t is the response variable or variable of interest at time *t* (in our case, $y_t = N_{t+1,1}$), x_{it} is the value of the *i*th input covariate series at time *t* (such as environmental variables or spawn index), μ_y and μ_{xi} are the means of y_t and x_{it}, respectively, and a_t is the white noise or random error component, assumed to be normally independently distributed (NID) with mean 0 and variance σ_a^2.

The transfer function components of the model, $\omega_i(B)\{\delta_i(B)\}^{-1} B^{b_i}$, are represented as finite-order polynomials such that

$$(8a) \quad \omega_i(B) = \omega_{0i} - \omega_{1i} B - \omega_{2i} B^2 - \ldots - \omega_{u_i i} B^{u_i}$$

$$(8b) \quad \delta_i(B) = 1 - \delta_{1i} \mathrm{B} - \delta_{2i} B^2 - \ldots - \delta_{r_i i} B^{r_i}$$

where ω_{ji}, $j = 0, 1, \ldots, u_i$, and δ_{ki}, $k = 1, 2, \ldots, r_i$, are parameters to be estimated, u_i and r_i are the orders of the polynomials $\omega_i(B)$ and $\delta_i(B)$, respectively, and B is the backward shift operator such that $Bz_t = z_{t-1}$ and $B^n z_t = z_{t-n}$ where *n* is a positive integer. The term B^{b_i} is used to account for any delay in the response associated with the *i*th covariate series.

The stochastic noise component of the model, $\theta(B)\{\phi(B)\}^{-1}a_t$, is used to model the autocorrelation structure associated with the data. This term includes a moving average operator of order q (MA(q)), $\theta(B)$, and an autoregressive operator of order p(AR(p)), $\phi(B)$, given by

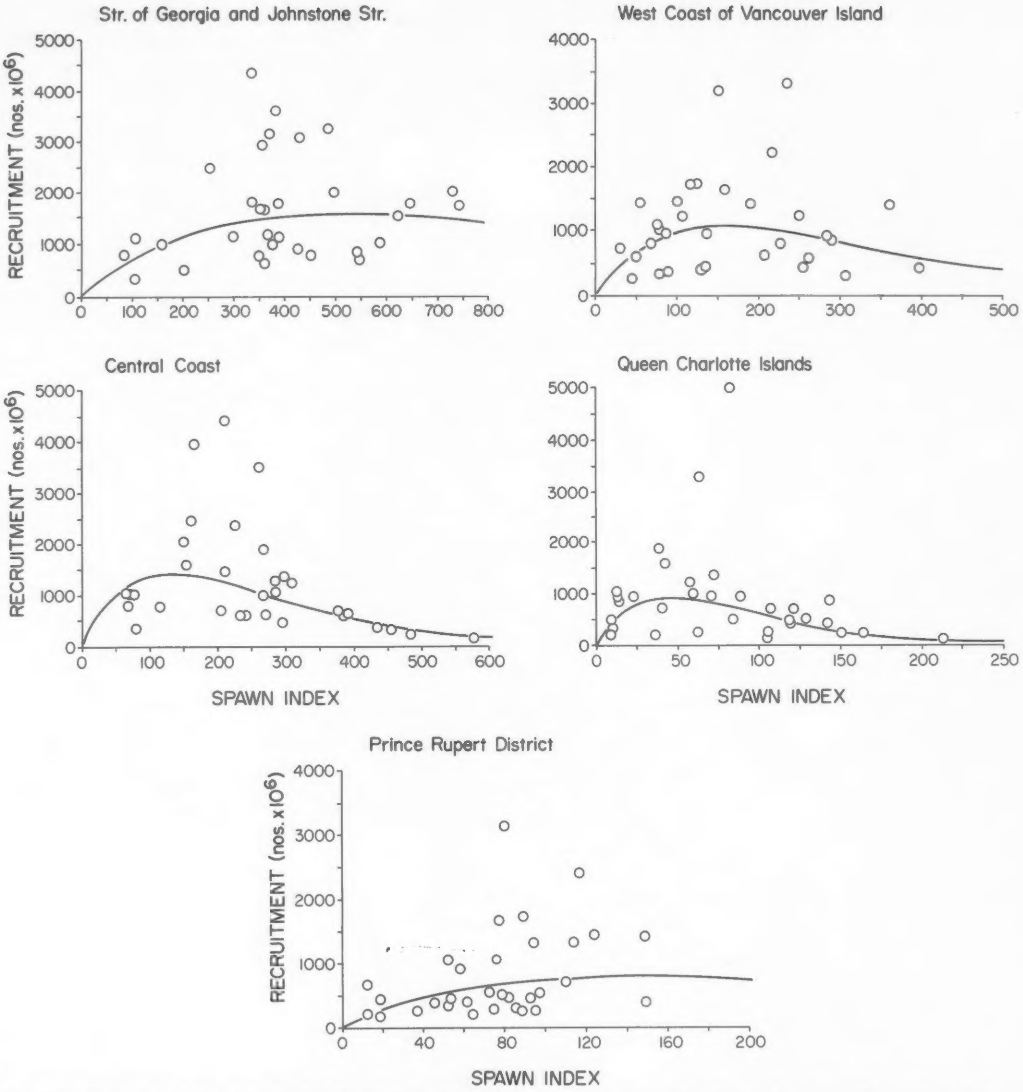

FIG. 1. Stock–recruit relationships for five British Columbia herring stock groupings. The abscissa is estimated recruitment, $N_{t+1,1}$, and the ordinate is spawn index, S_t. The solid line is the average stock–recruitment relationship plotted from the parameter estimates of α and β for the Ricker model (equation (1)).

$$(9)\quad \theta(B) = 1 - \theta_1 B - \theta_2 B^2 - \ldots - \theta_q B^q$$

and

$$(10)\quad \phi(B) = 1 - \phi_1 B - \phi_2 B^2 - \ldots - \phi_p B^p,$$

respectively. The combined term is referred to as an ARMA (p,q) process.

ARMA models have been used by other researchers to model fisheries data (e.g. Jensen 1976, 1985; Noakes 1986; Pennington 1985; Saila et al. 1980). In an AR process, the observation at time t is related in a linear fashion to observations before time t. An MA process expresses the response variable, y_t, in terms of previous error terms. Mixtures of AR and MA processes result in a convenient and compact method of describing the autocorrelation structure present in a particular time series.

In practice, only subsets of the general model (7) will be used to describe the relationship between stock and recruitment. The practitioner's job is to identify tentative candidate models and to select the most appropriate model from the set of models passing sensitive diagnostic checks. In this paper, cross-correlation analyses together with a general understanding of the physical and biological processes involved were employed to determine the covariate series to be included in the tentative models. The residuals associated with each of the tentative models were then calculated assuming $\theta(B)\{\phi(B)\}^{-1} = 1$. The orders of the AR and MA operators were then selected by examining plots of the autocorrelation function (ACF) and partial autocorrelation function (PACF) (Box and Jenkins 1970). Finally, the parameters associated with the transfer function and

TABLE 2. Environmental variables included in the environmental-dependent Ricker stock–recruitment models for five herring stock groupings.

Stock grouping	Variables
Strait of Georgia/ Johnstone Strait	SST, February – March mean sea surface temperature, Entrance Island FRASER, February – March mean discharge Fraser River at Hope SLEV, November – December mean sea level, Point Atkinson
West Coast of Vancouver Island	SST, February, April, September–December mean sea surface temperature, Amphitrite Point SAL, March mean salinity, Amphitrite Point SLEV, June – July mean sea level, Tofino
Central Coast	SST, November – December mean sea surface temperature, Cape St. James
Queen Charlotte Islands	SAL, January mean salinity, McInnes Island
Prince Rupert district	SST, May – September mean sea surface temperature, Cape St. James TRANS, sum of January and February Ekman transport, 54°N, 134°W SLEV, January mean sea level, Prince Rupert

TABLE 3. Covariate series and ARMA terms included in the TFN models used to forecast herring recruitment for the five stock groupings. Stock-specific environmental variables employed in the TFN models correspond to those presented in Table 2. SI = spawn index; SST = sea surface temperature; TRANS = Ekman transport; ϕ_1 = first-order autoregressive parameter; 0 = not included in the model; 1 = included in the model.

Stock grouping	SI	SST	TRANS	ϕ_1
Strait of Georgia/ Johnstone Strait	0	0	0	1
West Coast of Vancouver Island[a]	0	1	0	1
Central Coast	1	1	0	0
Queen Charlotte Islands	0	0	0	0
Prince Rupert district	1	1	1	1

[a] Series differenced once.

stochastic noise components were estimated simultaneously to provide the overall model. In all cases, the model residuals were analyzed to ensure that they were not significantly autocorrelated and were approximately NID.

It is interesting to note that both the Ricker stock–recruitment model (1) (Ricker 1954) and Cushing's power model of stock and recruitment (Cushing 1973) are essentially special cases of the general TFN model (7). Assuming the time series have been mean corrected, the necessary assumptions for both the Ricker and Cushing model are given in Table 1. Incorporating environmental information (e.g. SAL, SST, SLEV, etc.) is easily accomplished by including an additional transfer function component in the overall model.

A key advantage of the TFN model approach is that all candidate models are from a single class of models. A selection criterion such as the Akaike information criterion (AIC) (Akaike 1974) can be employed to select the "best" model from the set of models passing diagnostic checks. The AIC is defined as

$$(10)\quad \text{AIC} = -2(\text{maximized log likelihood}) + 2k$$

where k is the number of estimated parameters. The AIC provides a combined measure of good statistical fit and model parsimony, and the model with the minimum AIC value should generally be selected as the most appropriate.

Forecasting Evaluation Procedure

An objective criterion is necessary to compare the ability of competing models to generate accurate forecasts. This criterion, presumably, should reflect the expected cost(s) associated with the forecast error (e_t) and would ideally be zero at $e_t = 0$, be symmetric about zero, and increase monotonically for $|e_t| > 0$. Such assumptions are arguable for recruitment forecasting. For instance, overestimating recruitment could result in overfishing (a short-term gain) and a decrease in future recruitment (long-term loss). Underestimating recruitment could result in lost income opportunities for fishermen that may or may not be compensated by increased future harvest. Although the two costs likely increase monotonically for $|e_t| > 0$, it is not immediately obvious that they should be symmetric about $e_t = 0$.

The development of an appropriate cost function is a management decision and is beyond the scope of this paper. In practical terms, nonsymmetric cost functions may introduce a bias to the forecast but are unlikely to drastically affect the selection of the "best" forecasting model (Granger and Newbold 1977). In this paper, we consider five symmetric, monotonically increasing cost functions to compare the four competing models: (1) root mean squared error (RMSE), (2) mean absolute percent error (MAPE), (3) mean absolute deviation (MAD), (4) median absolute percent error (Median APE), and (5) median absolute deviation (Median AD). The median values were employed to decrease the influence of a single or a few large errors. In particular, very large percent errors result when observed values are small (Noakes et al. 1985).

To test the forecasting power of the four methods, we used five cost functions or performance measures described above. For each of the five stock groupings we have a time series of data as follows:

Stock grouping	Data set	Forecasts
St. of Georgia/Johnstone St.	1951–82	1976–82
West Coast Vancouver Island	1951–81	1975–81
Central Coast	1951–82	1976–82
Queen Charlotte Islands	1951–82	1976–82
Prince Rupert district	1951–82	1976–82

The four methods were used to generate 35 one-step-ahead forecasts (seven forecasts for each series) of year-class strength ($\hat{N}_{t+1,1}$). For example, for the Central Coast we forecast $\hat{N}_{1976,1}$ based upon data from 1951–75. We then advance 1 yr, use data from 1951–76 to update the parameter estimates for each model, and forecast $\hat{N}_{1977,1}$. We repeat this procedure through to $\hat{N}_{1982,1}$, and calculate the performance measure such as

$$(11)\quad \text{RMSE} = \frac{1}{7}\sum_{t=1975}^{1981}(N_{t+1,1} - \hat{N}_{t+1,1})^2$$

where $N_{t+1,1}$ is estimated year-class strength from the age-structured model analysis.

TABLE 4. Recruitment forecasts of four methods for five Pacific herring stock groupings.

			$\hat{N}_{t+1,1}$ ($\times 10^6$) Forecast method			
Stock grouping	Year of forecast	Estimated $N_{t+1,1}$ ($\times 10^6$)	Ricker	Ricker environmental	Mean	TFN
St. of Georgia/ Johnstone Strait	1976	693	2338.27	3173.49	1869.36	1726.25
	1977	1007	2205.17	1569.94	1824.12	1035.76
	1978	830	2097.22	2878.04	1793.85	1308.47
	1979	895	1982.33	1689.91	1759.43	1135.92
	1980	775	1956.29	1483.49	1729.62	1176.73
	1981	764	1820.69	811.92	1697.80	1050.73
	1982	617	1799.82	925.97	1667.68	1023.00
West Coast of Vancouver Island	1975	1384	1402.48	1652.08	1111.71	1058.60
	1976	394	1408.56	1653.62	1122.60	1316.94
	1977	906	1290.03	1221.96	1094.58	580.72
	1978	560	1299.45	1074.57	1087.59	710.16
	1979	415	1249.40	1030.09	1068.75	678.49
	1980	279	1059.36	859.14	1046.21	475.43
	1981	595	1201.56	535.17	1020.63	325.45
Central Coast	1976	368	766.96	648.98	1385.56	1083.03
	1977	3524	1333.34	1387.09	1346.42	1313.61
	1978	597	1493.52	1244.32	1427.07	1095.07
	1979	598	1484.36	867.09	1397.43	813.13
	1980	226	566.98	396.14	1369.86	841.22
	1981	147	300.59	170.41	1331.73	599.43
	1982	319	513.35	449.73	1293.52	777.94
Queen Charlotte Islands	1976	215	395.57	369.35	775.67	775.67
	1977	4999	884.79	757.52	750.18	750.18
	1978	244	821.39	384.62	934.91	934.91
	1979	129	768.98	181.41	906.13	906.13
	1980	84	114.6	85.44	875.04	875.04
	1981	846	389.41	635.11	844.62	844.62
	1982	236	319.27	305.80	844.67	844.67
Prince Rupert District	1976	234	1006.14	481.71	810.08	383.10
	1977	1652	922.83	1699.34	787.92	824.10
	1978	365	716.73	1387.09	819.93	1371.30
	1979	326	758.33	556.42	803.68	354.12
	1980	436	982.30	1242.54	787.21	1105.15
	1981	1302	1007.76	2354.72	775.50	1796.31
	1982	514	995.49	643.97	792.48	548.87

Finally, to evaluate the methods, rank and rank-sum comparisons were made. Each of the four models was assigned an integer rank from 1 to 4 to indicate forecast performance from "best" to "worst." Rank-sums were then computed for each performance measure by multiplying the number of times a particular model was assigned a given rank by that rank and summing over all ranks. For instance, if a given model received a rank of 1 three times and a rank of 4 twice, its rank-sum would be $3 \times 1 + 2 \times 4 = 11$.

Results

Ricker Models

The stock–recruitment histories of the five British Columbia herring stock groupings (Fig. 1) show that the stocks have experienced strong fluctuations in recruitment success over the study period. This behaviour suggests that density-independent (environmental) factors may be significantly influencing recruitment. Environmental variables included in the Ricker environmental models are those that showed significant "exploratory correlations" with recruitment estimates of the five stock groupings (Table 2).

The covariate series and ARMA terms included in the TFN models used to forecast herring recruitment for the five stock groupings are presented in Table 3. All recruitment data in this study were transformed by taking natural logarithms. The log transformation was needed to ensure that the model residuals were approximately normally distributed and homoscedastic. Herring recruitment in the Queen Charlotte Islands appeared to

TABLE 5. Summary of recruitment forecast errors for seven one-step forecasts and ranks assigned to each of the forecasting methods for five British Columbia herring stocks.

		Forecast method							
		Ricker		Ricker environmental		Mean		TFN	
Stock grouping		Performance measures	Rank	Performance measures	Rank	Performance measures	Rank	Performance measures	Rank
Strait of Georgia/ Johnstone Strait	RMSE	1244.52	3	1303.61	4	972.11	2	501.97	1
	MAD	1231.26	4	993.11	3	965.84	2	410.84	1
	Median AD	1183.00	4	708.00	2	955.00	3	401.73	1
	MAPE	159.00	4	128.17	3	125.61	2	55.96	1
	Median APE	152.40	4	89.00	2	122.20	3	51.84	1
West Coast of Vancouver Island	RMSE	696.63	4	625.83	3	549.82	2	425.39	1
	MAD	625.41	4	516.18	3	509.09	2	350.46	1
	Median AD	739.00	4	515.00	2	528.00	3	269.55	1
	MAPE	145.14	4	118.86	3	117.67	2	71.38	1
	Median APE	132.00	4	92.00	2	94.20	3	45.30	1
Central Coast	RMSE	980.17	3	860.51	1	1240.22	4	962.53	2
	MAD	723.06	2	522.65	1	1161.11	4	737.89	3
	Median AD	399.00	2	269.00	1	1018.00	4	498.07	3
	MAPE	112.18	2	60.37	1	318.37	4	157.18	3
	Median APE	108.40	2	60.60	1	277.00	4	143.87	3
Queen Charlotte Islands[a]	RMSE	1599.94	1	1607.39	2	1708.98	3.5	1708.98	3.5
	MAD	868.95	2	695.86	1	1096.94	3.5	1096.94	3.5
	Median AD	457.00	2	141.00	1	691.00	3.5	691.00	3.5
	MAPE	146.39	2	44.45	1	347.31	3.5	347.31	3.5
	Median APE	82.00	2	40.60	1	261.00	3.5	261.00	3.5
Prince Rupert district	RMSE	541.87	2	647.74	4	533.42	1	587.29	3
	MAD	515.34	4	505.26	3	504.14	2	458.53	1
	Median AD	481.00	3	248.00	1	478.00	2	494.31	4
	MAPE	120.67	4	107.22	3	106.40	2	85.20	1
	Median APE	96.00	4	80.90	3	80.60	2	50.12	1

[a] The mean was used as a forecast for the Queen Charlotte Islands TFN model. As a result the same ranks were assigned to the mean and TFN methods.

TABLE 6. Rank-sums for the competing forecasting procedures and performance measures. Lower rank-sums and totals indicate better overall performance.

Performance measure	Ricker	Ricker environmental	Mean[a]	TFN[a]
RMSE	13	14	12.5	10.5
MAD	16	11	13.5	9.5
Median AD	15	7	15.5	12.5
MAPE	16	11	13.5	9.5
Median APE	16	9	15.5	9.5
Total	76	52	70.5	51.5

[a] The mean was used as a forecast for the Queen Charlotte Island stock for the TFN model.

be strictly random. Thus, in this case, the forecasts generated by the TFN model were simply the means.

Forecasting Evaluation

As noted previously, the forecasts generated by the running average and TFN models (Table 4) were identical for the Queen Charlotte Island stock. In general, all models tended to overestimate recruitment. This is not surprising, since it appears that recruitment during the 1976–82 period is somewhat below long-term average recruitment levels (compare columns $N_{t+1,1}$ and Mean in Table 4).

The forecast errors associated with each of the four models were compared using the five performance measures RMSE, MAD, Median AD, MAPE, and Median APE (Table 5). The models were ranked for each performance measure and stock grouping. A rank of 1 was assigned to the model that forecasted "best" for a particular performance measure and a rank of 4 to the "worst" model. The TFN model provided the "best" forecast of recruitment for the Strait of Georgia/Johnstone Strait and West Coast of Vancouver Island stocks. In both stocks, there appeared to be a 30–50% reduction in expected error for the TFN model compared with the competing forecasting procedures (all performance measures). The Ricker environmental model performed well for the Central Coast and Queen Charlotte Island stocks except for one notable exception. The RMSE's for the Queen Charlotte Island stock were all very close, and on this basis one might conclude that there is little reason to give any one model preferential consideration. However, the Ricker environmental model did provide "better" forecasts when the other performance measures were compared. There appears to be no clear choice for the Prince Rupert district stock, as all four models performed equally well or

TABLE 7. Forecasts of the 1984 year-class strengths for five British Columbia herring stock groupings. RE = Ricker environmental.

		Forecast year-class strength			Corresponding forecast of 3-yr-old biomass		
Stock grouping	Method	Year	$\hat{R}$ ($N \times 10^6$)	50% C.I.	Year	$\hat{B}$ (tonnes)	Range
Strait of Georgia/ Johnstone Strait	TFN	1984	1124	828–1527	1987	22559	14175–28411
West Coast of Vancouver Island	TFN	1984	793	565–1112	1987	13806	10519–18426
Central Coast	RE	1984	1132	793–1615	1987	15450	11264–22537
Queen Charlotte	RE	1984	646	387–1078	1987	8050	5508–15173
Prince Rupert district	MEAN	1984	784	300–1268	1987	7583	2243–8723

poorly depending on whether one adopts an optimistic or pessimistic outlook.

Rank-sums were computed for each performance measure by multiplying the number of times a given model receives a specific rank by that rank and summing over all ranks (Table 6). For example, consider the performance of the Ricker model using the RMSE criterion. The Ricker model received ranks of 1, 2, and 4 once and a rank of 3 twice (Table 5). The rank-sum for the Ricker model using RMSE is thus $1 \times 1 + 1 \times 2 + 2 \times 3 + 1 \times 4 = 13$. Note that for the Queen Charlotte Island stock, the mean was used as the forecast for the TFN model and therefore received the same rank as the mean model (3.5 for all performance criterion). Models with lower rank-sums performed better overall than those with higher rank-sums. The TFN model had the lowest rank-sum for the RMSE, MAD, and MAPE performance criteria, while the Ricker environmental model had the lowest rank-sum for the Median AD and Median APE. The TFN and Ricker environmental models performed equally well overall with total rank-sums of 51.5 and 52, respectively.

To show the level of certainty attached to forecasts, the "best" models for each stock grouping are used to make a numerical forecast of year-class strength with 50% confidence intervals. For example, the 1984 year-class should produce 14 000–28 000 tonnes of 3-yr-olds in 1987 for the Strait of Georgia/Johnstone Strait (Table 7).

Discussion

The ability of four types of models to forecast herring recruitment has been examined in this paper. A time series approach provided the best forecasts for the two southern most stocks, the Strait of Georgia/Johnstone Strait and West Coast of Vancouver Island. A Ricker stock–recruitment model that takes into account environmental data produced marginally better forecasts than the three other competing models for the Central Coast and Queen Charlotte Island stocks. The four models produced approximately equally good or poor forecasts of herring recruitment for the Prince Rupert district stock.

Five performance measures were used to generate ordinal rankings for the four models in each of the five stock areas. The rankings were generally consistent for the five performance measures with the exception of the Prince Rupert district stock. In this instance, all models produced equally good/poor forecasts of herring recruitment with very little difference between the best and worst forecasts. The rankings presented in this paper are meant to provide guidance to managers given the task of selecting a model to generate forecasts of recruitment. The series are too short to test for statistically significant differences in the forecast errors.

The TFN model performed best for the south coast stock groupings. Although it is not immediately obvious from a biological perspective why this should occur, there are certain characteristics of the data that could help account for such behaviour. First, these stocks have been declining due to a series of weak year-classes from 1976 to 1981. In fact, the decline in the West Coast of Vancouver Island stock was so pronounced that the recruitment series required differencing to remove this trend prior to fitting a time series model to the data (Table 3). The lag 1 autocorrelation for the Strait of Georgia/Johnstone Strait stock was quite large (ϕ, > 0.7). Since time series models are particularly well adapted for handling trends and autocorrelated data, it is not surprising that they produced better forecasts for these two stocks than the mean, Ricker, and Ricker environmental models.

The same data characteristics were not apparent in the other three stocks considered in this study. There were no strong trends or autocorrelations present in the recruitment time series for these stocks. In the absence of these factors, there is little reason to expect time series models to generate better forecasts than the other competing techniques. This is precisely what happened in the study. The Ricker environmental model produced marginally better forecasts for the Queen Charlotte Island and Central Coast stocks, while all models performed equally well/poorly for the Prince Rupert district stock. The signal to noise ratio for the Prince Rupert stock was at such a low level that the running average provided as good a forecast of recruitment as any of the models considered in the study.

Undoubtedly, some will argue that time series models are black boxes and may not provide significant insight into the underlying biological and physical processes. However, two important points should be considered before such models are dismissed. First, managers are faced with the reality of generating short-term forecasts in order to establish annual quotas according to some specified management strategy. For species such as herring, new recruits can represent a substantial proportion of the biomass, and any improvement in forecast accuracy is important. While developing forecasting models from sound biological principles is desirable, we simply do not have the luxury of time to establish all of the key biological and physical interactions (even if this were possible). Second, these time series models have served well in practice in the past (e.g. see Granger and Newbold 1977; Makridakis et al. 1982; McLeod et al. 1987; Noakes et al. 1985; Noakes et al. 1988).

Therefore, until better methods of forecasting are found, these models should be retained for use in the future.

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Are Growth Parameters Estimated from Tagging and Age–Length Data Comparable?

R. I. C. C. Francis

Fisheries Research Division, Ministry of Agriculture and Fisheries, P.O. Box 297, Wellington, New Zealand

Francis, R. I. C. C. 1988. Are growth parameters estimated from tagging and age–length data comparable? Can. J. Fish. Aquat. Sci. 45: 936–942.

The two most common ways of estimating fish growth use age–length data and tagging data. It is shown that growth parameters estimated from these two types of data have different meanings and thus are not directly comparable. In particular, the von Bertalanffy parameter l_∞ means asymptotic mean length at age for age–length data, and maximum length for tagging data, when estimated by conventional methods. New parameterizations are given for the von Bertalanffy equation which avoid this ambiguity and better represent the growth information in the two types of data. The comparison between growth estimates from these data sets is shown to be equivalent to comparing the mean growth rate of fish of a given age with that of fish of length equal to the mean length at that age. How much these growth rates may differ in real populations remains unresolved: estimates for two species of fish produced markedly different results, neither of which could be reproduced using growth models. Existing growth models are shown to be inadequate to answer this question.

Les deux façons les plus courantes d'évaluer la croissance des poissons sont fondées sur les données de longueur par rapport à l'âge et sur les données de marquage. Il est montré que les paramètres de croissance estimés par ces deux types de données prennent une signification différente et ne sont donc pas directement comparables. C'est le cas notamment du paramètre l_∞ de von Bertalanffy qui donne la longueur moyenne asymptotique pour un âge donné quand on applique les données de longueur par rapport à l'âge, mais qui donne la longueur maximum quand on applique les données de marquage et que les estimations sont faites par des méthodes classiques. De nouveaux paramètres applicables à l'équation de von Bertalanffy sont proposés; on pourrait ainsi éviter l'ambiguïté dont il est question et obtenir une meilleure représentation des renseignements sur la croissance que ces deux types de données contiennent. Il est montré que la comparaison des deux évaluations correspond à comparer le taux de croissance moyen des poissons à un âge donné à celui de poissons dont la longueur est égale à la longueur moyenne pour cet âge. On ne sait pas dans quelle mesure ces taux de croissance peuvent différer dans des populations réelles; l'estimation chez deux espèces a donné des résultats très différents qui n'ont pu être reproduits avec des modèles de croissance. Il est montré que les modèles de croissance actuels ne nous permettent pas de répondre à cette question.

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The description of growth is a basic problem in population biology. For fish populations this usually means growth in length, and the two most common ways of estimating this are using age–length data (Tomlinson and Abramson 1961; Kimura 1980) and via length increment data derived from tagging experiments (Fabens 1965). Both approaches have some problems: ageing methods are often imprecise and difficult to validate (Beamish and McFarlane 1983), and fish growth may well be affected by tags (Kelly and Barker 1963; Saunders and Allen 1967; Jakobsen and Jákupsstovu 1977). Thus it is of interest to compare growth parameters estimated by the two methods. The question is: are these two sets of parameters directly comparable?

Sainsbury (1980) approached this question (see his fig. 3) when considering populations in which growth is described by a von Bertalanffy curve and each individual has its own parameters. Kirkwood (1983), in proposing a method of estimating von Bertalanffy growth using length increment and age–length data together, raised the question without answering it, and concluded (p. 1410) "This topic certainly deserves further research."

In this paper I show (firstly for the case of von Bertalanffy growth, and then by generalisation to all growth curves) that the answer to the question is "no" and suggest new parameters for the von Bertalanffy growth curve which follow from this result. Modelling and direct estimation from empirical data are used in an attempt to quantify likely differences between the two types of growth estimates.

In what follows, "age–length data" means a single age and length for each of a set of individuals and "tagging data" means a time and length at tagging and at recapture for each of a set of individuals. Ages and times are measured in years. There are a number of factors (such as variations in year-class strength and within- and between-year differences in growth rates) which may lead to different growth estimates from "snap-shot" (e.g. age–length) data and extended time period (e.g. tagging) data. Although these factors are important, and must be considered in comparing growth parameters from the two types of data, they will be ignored here because the differences discussed below will occur even in their absence.

von Bertalanffy Growth

I first show that the conventional models used in fitting the von Bertalanffy curve to the two types of data are not equivalent — in particular the traditional parameters have different meanings in the two models.

The usual forms of the von Bertalanffy equation, as used with age–length and tagging data, are

$$(1) \quad L = l_\infty(1-e^{-k(T-t_0)})$$

and

$$(2) \quad \Delta L = (l_\infty - L)\,(1-e^{-k\Delta T})$$

respectively. Both forms use the usual von Bertalanffy parameters, l_∞, k, and t_0, to relate other variables: the former relating length, L, to age, T; the latter relating length increment, ΔL, to length (at tagging), L, and time at liberty, ΔT. Since (2) may be derived from (1) (e.g. see Fabens 1965), it seems reasonable to assume that the parameters l_∞ and k will have the same meaning in both equations (t_0 is not estimable from tagging data and so will not be considered further here). However, this is not the full story; the meanings of these equations are not fully described until the methods of fitting them are specified.

Whether (1) is fitted by least squares (Tomlinson and Abramson 1961) or maximum likelihood (Kimura 1980) the implication is the same: L is to be thought of as the expected (or mean) length at observed age T, and the fitting procedure simply selects parameter values to minimise (in some sense) the difference between the observed and expected values of L for each observed T. Similarly, the least squares method of Fabens (1965), which uses (2), implies that ΔL is the expected length increment for observed length L and time at liberty ΔT. Notice that L is an expected length in (1) and an observed length in (2). In the derivation of (2) from (1), this change of meaning of L is usually ignored. Thus (1) and (2), as conventionally interpreted, are different models and not simply different formulations of the same model. We cannot assume that if one of these models holds for a given population, then so does the other. (An example is given below in which model (1) is true but model (2) is not.)

Alternative ways of using (2) illustrate how the fitting method affects the interpretation of the variables. A rearrangement of (2) would allow the calculation of L for a given ΔL and ΔT. The parameters l_∞ and k could then be chosen to minimise the differences between this "expected" L and the observed L. L would then be interpreted as the mean length of all fish which grow ΔL over time period ΔT. Yet another interpretation of (2) is implied by Kirkwood (1983, equation 3). Thus, equation (2) can be used for (at least) three different growth models, each implying its own interpretation of L, ΔL and ΔT.

Having established that models (1) and (2) are different, and not merely different forms of the same model, I now shew that the biological meanings of l_∞ and k (where they have any) are different in the two models. To aid the demonstration, I will denote their meanings in the age–length and tagging models by $l_{\infty,a}$ and k_a, and $l_{\infty,t}$ and k_t, respectively. From model (1) it follows that $l_{\infty,a}$ is the asymptotic mean length at age or, loosely speaking, the mean length of "old" fish (where "old" means of an age beyond which the mean length at age does not increase appreciably). This has biological meaning only in populations in which the mortality is low enough to allow fish to reach an age at which the mean length (virtually) ceases to increase. Because of variability in individual growth, we should expect some "old" fish to have lengths $>l_{\infty,a}$. Not all such fish will have stopped growing, so the expected growth increment for these fish over some given period will be >0. In model (2), expected growth increments are positive only for fish of lengths $<l_{\infty,t}$. Thus if models (1) and (2) both hold true, $l_{\infty,t}$ must be $>l_{\infty,a}$, i.e. $l_{\infty,a} \neq l_{\infty,t}$. Since $l_{\infty,t}$ is the length for which the expected growth increment (for any given time period) is zero, it must be the maximum length achieved in the population (unless negative growth is common). (This interpretation may be questioned by researchers who have data which produce an estimate of $l_{\infty,t}$ that is lower than the maximum observed length. This, I suggest, is simply evidence that the model is inappropriate. On the other hand, if fish die well before reaching length $l_{\infty,t}$, then this parameter can have no biological meaning.)

For both models the meaning of k is dependent on l_∞. For example, in (1), k is a relative growth rate descriptor which may be characterised by saying that the time for the mean length of an age-class to increase halfway to l_∞ from any starting length is $(\log_e 2)/k$. This connection between k and l_∞ implies that, since $l_{\infty,a} \neq l_{\infty,t}$, $k_a \neq k_t$. Thus, for conventional applications of the von Bertalanffy equation, the answer to the question posed by this paper is "no."

Growth Curves in General

I now show, by a more general argument, that the conclusions of the preceding section apply to all growth curves.

Consider an ideal population in which the age and length distributions do not vary over time, and suppose we could record, at one instant, the age and length of every fish. From these data we could draw an exact mean length at age curve, and if this curve was of a known parametric form (such as (1)), we could calculate exact values for the parameters. We may find, for example, that the mean lengths of 2- and 3-yr-old fish were 20 and 25 cm, respectively, so the mean annual growth of 2-yr-old fish is 5 cm. However, this is not the same as saying that the expected annual growth of 20-cm fish is 5 cm; in fact we cannot make any precise estimate of this growth rate, since our age and length data do not contain any direct observations of growth. Thus even the very fullest of age–length data sets does not contain precise information on the expected growth rate of fish of a given length (which is what is estimated from tagging data).

The conclusion to be drawn is that the two types of data, and thus the parameters estimated from them, contain different growth information — age-based for age–length data and length-based for tagging data. Furthermore, a comparison between growth parameters estimated from these data types is equivalent to comparing growth rates at age with growth rates at length (Fig. 1). These are not the same thing, so the answer to the question posed by this paper is "no."

In the preceding section it was shown that, where it has biological meaning, l_∞ means different things in models (1) and (2). The argument of this section indicates that the growth information in l_∞ must differ in the two models regardless of the issue of biological meaning.

An Example

In this section a simple population growth model is presented that demonstrates explicitly that the usual von Bertalanffy tag-

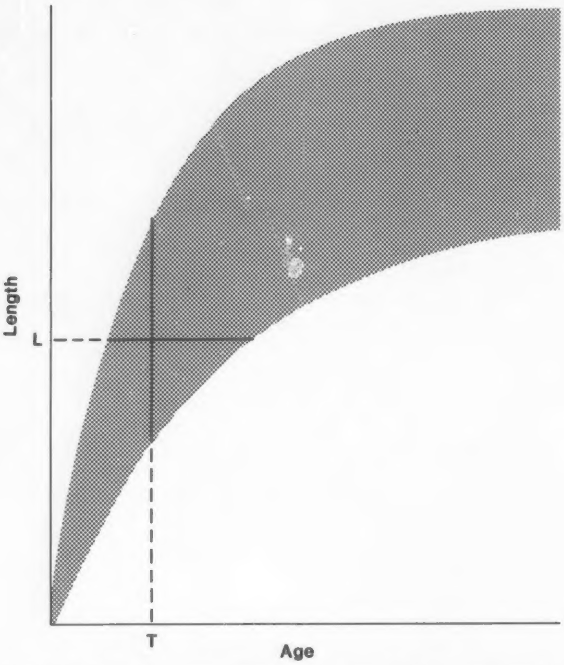

FIG. 1. Schematic diagram illustrating the nature of the comparison of growth parameters estimated from age–length and tagging data. This comparison is equivalent to identifying the mean growth rate of fish of age T (those on the vertical line) with that of fish of length L (those on the horizontal line), where L is the mean length of fish of age T. The shaded area indicates the range of ages and lengths in the population.

ging growth model, (2), is not equivalent to the conventional age–length growth model, (1). The difference between age- and length-based growth rates will also be shown.

Consider a population of the type described by Sainsbury (1980) in which the ith fish has its own set of von Bertalanffy parameters ($l_{\infty i}$, k_i, t_{0i}) which it retains throughout life and which describes exactly its growth. We will assume that (i) for all fish, $k_i = k$ and $t_{0i} = 0$, (ii) at birth, the distribution of $l_{\infty i}$ is uniform over the interval ($l_\infty - c$, $l_\infty + c$), and (iii) the fish are subject to a constant total instantaneous mortality Z.

The inclusion of a mortality term in this model may seem surprising, but its role here is easily explained. Consider a sample of fish all of the same length. The younger fish in this sample must have higher growth rates and thus higher values of l_∞ than the older fish. Thus the mean growth rate in this sample will depend on the relative proportions of younger and older fish, and this in turn depends on the mortality rate: a high mortality rate implies a high proportion of young fish. Thus we see that Z affects length-based growth rates but not (because fish of the same age have experienced the same mortality) age-based rates.

Under these assumptions it may be shown that the mean length, L, of fish of age T is given by (1). Calculation of the expected length increment, ΔL, for a fish of initial length L, over time period ΔT, is more complicated, but for the special case when $Z = k$ it may be shown (details available from the author) to be given by an equation similar to (2):

$$(3)\quad \Delta L = (\lambda - L)(1 - e^{-k\Delta T})$$

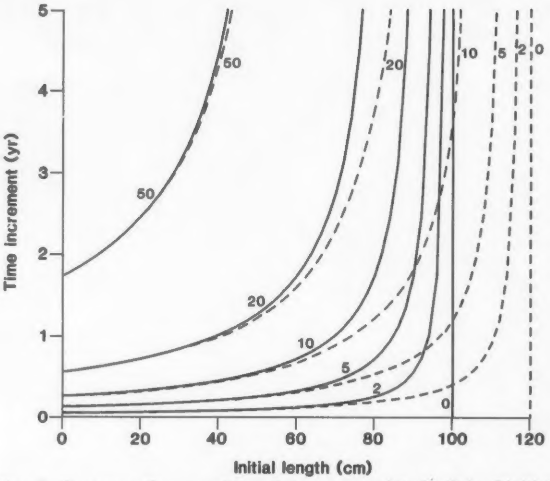

FIG. 2. Contours of expected length increment, ΔL, for fish of initial length, L, over time period ΔT, for equations (2) (solid lines) and (3) (broken lines), with $l_\infty = 100$ cm, $c = 20$ cm, and $k = 0.4 \cdot \text{yr}^{-1}$. Numbers by contour lines are values of ΔL.

where

$$\lambda = \begin{cases} (l_\infty - L)/[1 - L\log((l_\infty + c)/(l_\infty - c))/(2c)] & \text{if } L < l_\infty - c \\ 0.5(l_\infty + c - L)/[1 - L\log((l_\infty + c)/L)/(l_\infty + c - L)] & \text{if } L > l_\infty - c. \end{cases}$$

(λ is not another parameter, it is simply a notational convenience which allows us to see the similarity between (2) and (3).)

This makes it clear that the tagging model, (2), is not implied by the age–length model, (1). The difference between (2) and (3) is shown in Fig. 2 for the case where $l_\infty = 100$ cm, $c = 20$ cm, and $k = 0.4 \cdot \text{yr}^{-1}$.

From (1) we may calculate that fish of age 3 have an average length of 69.9 cm and an expected annual growth of 9.9 cm. By contrast, the expected annual growth for fish of length 69.9 cm is, from (3), 11.0 cm. The first of these two growth rates (which is age-based) is what would be estimated from age–length data; the second (length-based) is estimable from tagging data. The comparison of growth parameters derived in the conventional ways from age–length and tagging data tacitly assumes that the two growth rates are equal.

In this example a simplistic model has been used to demonstrate explicitly the difference between age- and length-based growth. In a later section a more realistic version of the model will be used in an attempt to describe the probable size of the difference.

Parameterizing Growth

It is unsatisfactory (and confusing) to use growth parameters such as l_∞ and k which, as has been shown above, have different meanings depending on whether they are estimated from age–length or tagging data. In this section, I suggest, for the von Bertalanffy equation, parameters that avoid this ambiguity and better represent the data from which they are to be estimated.

Consider the following reparameterizations of the two forms of the von Bertalanffy curve, (1) and (2):

$$(4)\quad L = l_\phi + (l_\psi - l_\phi)(1 - r^{2(T-\phi)/(\psi-\phi)})/(1 - r^2)$$

where

$$r = (l_\psi - l_\chi)/(l_\chi - l_\phi)$$

and

$$(5) \quad \Delta L = ((\beta g_\alpha - \alpha g_\beta)/(g_\alpha - g_\beta) - L) \div (1-(1+(g_\alpha - g_\beta)/(\alpha-\beta))^{\Delta T}).$$

In (4) the three usual von Bertalanffy parameters are replaced by l_ϕ, l_χ, and l_ψ, which are mean lengths at ages ϕ, $(\phi+\psi)/2$, and ψ for some arbitrary reference ages ϕ and ψ. (r is used only to simplify the presentation of (4); it is not another parameter.) The parameters g_α and g_β of (5) were devised by Francis (1988a) and are the mean annual growth increments of fish of arbitrary reference lengths α and β.

The new parameters are related to the conventional ones by the equations

$$l_{\infty,a} = l_\phi + (l_\psi - l_\phi)/(1-r^2)$$
$$k_a = -(2\log_e r)/(\psi - \phi)$$
$$t_0 = \phi + (1/k_a)\log_e((l_{\infty,a} - l_\phi)/l_{\infty,a})$$

for the age–length model, (1), and

$$l_{\infty,t} = (\beta g_\alpha - \alpha g_\beta)/(g_\alpha - g_\beta)$$
$$k_t = -\log_e(1+(g_\alpha - g_\beta)/(\alpha - \beta))$$

for the tagging model, (2).

An attractive feature of the new parameters is that they describe properties of a fish population (mean lengths at age and mean growth rates at length) which are directly observable in the corresponding data sets (age–length and tagging, respectively) and which exist independent of the von Bertalanffy equation. In this sense they may be said to be representative of the growth information in the data. By contrast, k is not directly observable and is a mathematical construct which has meaning only if growth in the population follows model (1) or (2). As used with model (1), l_∞ describes a population characteristic only if growth is asymptotic; for many published age–length data sets to which von Bertalanffy curves have been fitted, there is no evidence of this (e.g. Ralston and Miyamoto 1983, fig. 9; Kirkwood 1983, fig. 1; Knight 1968, fig. 2).

The reference ages (ϕ,ψ) and lengths (α,β) in these parameterizations must, of course, be chosen to lie within the range of the data: what would it mean to estimate l_7 from age–length data in which the maximum age was 5? This ensures that the parameter estimates are not extrapolations. It is worth commenting that the basis of Knight's (1968) criticism of the von Bertalanffy curve is simply that l_∞ is estimated by extrapolation (and often, as in his fig. 2, extreme extrapolation). He does not say so, but the estimation of t_0 (from age–length data) must also, by definition, involve extrapolation.

The choice of reference lengths or ages does not affect the growth curve fitted. For example the parameters $g_{20} = 10.0$ cm and $g_{50} = 7.0$ cm describe precisely the same growth curve as do $g_{25} = 9.5$ cm and $g_{45} = 7.5$ cm. If the former parameter values were estimated from a given tagging data set using reference lengths 20 and 50 cm, then the latter values would be estimated if reference lengths 25 and 45 cm were used (except perhaps for slight differences associated with the estimation process).

A further advantage of these parameters lies in their statistical properties. Firstly, if the reference ages or lengths are well chosen for the data, the parameter estimates will not show the high correlation which is common between l_∞ and k. I have illustrated this with empirical data for (5) (Francis 1988a). A second property of the parameters concerns the extent to which they behave like those from linear equations (e.g. showing low bias and low excess variance) when estimated from small samples. Ratkowsky (1986) called this behaviour "close to linear" and showed that, of eight parameterizations of (1), that of Schnute and Fournier (1980) was best in this respect. He did not consider the form presented here, (4), but since it is an extension of Schnute and Fournier's, it may be expected to have similar properties. He has also shown (D. A. Ratkowsky, CSIRO Division of Mathematics and Statistics, Tasmanian Regional Laboratory, Stowell Avenue, Hobart, Tasmania 7000, Australia, pers. comm.) that the parameters of (5) are close to linear.

When parameterizations (4) and (5) are used the comparison of growth estimates from age–length and tagging data should be made between the growth rates at a given age and growth rates at the corresponding length. How different these may be is the subject of the next section.

Extent of Growth Rate Differences

Two methods were used to gain some understanding of how large the differences between growth rates at length and at age may be: direct estimation from empirical data, and modelling. Direct estimates were made for two species, Pacific bonito (*Sarda chiliensis*) and sand flounder (*Rhombosolea plebeia*), and a growth model similar to that of Sainsbury (1980) was fitted to the former data.

Some further notation will be useful. Suppose γ is the mean length at age θ. Let GA_θ and GL_θ be the mean annual growth rates at age θ and at length γ, respectively, and let VA_θ and VL_θ represent the coefficients of variation (expressed as percentages) of lengths at age θ and of annual growth at length γ, respectively. I will show below how the degree of variability in growth (as measured by VA and VL) affects the difference between GA and GL.

Note that the letters "A" and "L" label parameters as being either age-based (and estimable from age-length data) or length-based (and estimable from tagging data). The age subscript, θ, used with VL and GL, is only a notational convenience, indicating, for example, the association between GA_θ and what might otherwise be written GL_γ. It does not imply that VL and GL are age-based parameters. Where no confusion will arise, subscripts will be omitted.

In terms of the parameters of (4) and (5), $\mathrm{GA}_\theta = l_{\theta+1} - l_\theta$ and $\mathrm{GL}_\theta = g_\gamma$. We are interested in the difference between these growth rates, which will be written GD_θ and expressed as a percentage of the former: $\mathrm{GD}_\theta = 100(\mathrm{GL}_\theta - \mathrm{GA}_\theta)/\mathrm{GA}_\theta$. Thus, in the above example, I found $\mathrm{GA}_3 = 9.9$ cm and $\mathrm{GL}_3 = 11.0$ cm and may calculate $\mathrm{GD}_3 = 11\%$.

VL_θ is the same as v in the tagging growth model of Francis (1988a, equation 5) where it was assumed to be independent of length.

Now I present the direct estimates of GD for bonito. Campbell and Collins (1975, p. 187) estimated the mean length at age curve for bonito as $L = 76.87(1 - \exp(-0.6215(T + 0.410)))$ (there is a misprint in that paper: "$t - 0.410$" should be "$t + 0.410$"). This implies that $l_1 = 44.9$ cm, $l_2 = 59.7$ cm, and $l_3 = 67.6$ cm, from which we may calculate $\mathrm{GA}_1 = 14.8$ cm and $\mathrm{GA}_2 = 7.9$ cm. Francis (1988a) analysed Campbell and Collins' (1975) bonito tagging data and obtained $g_{35} = 11.0\,(\pm 0.8)$ cm and $g_{55} = 7.5\,(\pm 0.8)$ cm. Using Francis (1988a, equation 3), this leads to GL_1 (= $g_{44.9}$) = 9.3 cm and GL_2 (= $g_{59.7}$) = 6.7 cm; so for bonito, the direct estimates are $GD_1 = -37\%$ and $GD_2 = -15\%$.

Similar calculations yielded direct estimates of $GD_1 = 43\%$ and $GD_2 = 16\%$ for female sand flounder. These were based on the age–length curve of Mundy (1968, p. 112) and the tagging growth analysis of Francis (1988b).

For both bonito and flounder, limitations in the range of the tagging data did not allow estimation of GL_θ for $\theta \geqslant 3$ yr.

The growth model used here was, as in the above example (and Sainsbury 1980), based on the assumption that each fish grows according to its own set of von Bertalanffy parameters. However, the assumptions concerning the distributions of the parameters were different: l_∞ and t_0 were assumed to be normally distributed; because l_∞ and k were allowed to be correlated (with correlation ρ), it was convenient to use a lognormal distribution for k in place of Sainsbury's (1980) gamma (both distributions prevent k being negative). As in the above example, (instantaneous) mortality, Z, was assumed to be independent of age and length.

Before this model could be fitted to the bonito data, direct estimates of VA and VL were required. The former was estimated by Francis (1988a) as 35 ($\pm$5)% over the range of the data. Since most fish were between 30 and 60 cm at tagging, we can say (using the above bonito growth curve) that VL_θ = 35% for $0.4 \leqslant \theta \leqslant 2$.

Estimates of VA for bonito were derived from Campbell and Collins (1975, fig. 4) in which is presented the range of lengths at each age in a sample of 3139 bonito. Firstly, a total instantaneous mortality $Z = 1 \cdot yr^{-1}$ was assumed (this implies 0.1% survival at age 7, which is consistent with the fact that the oldest fish in the sample was age 6+). It was assumed that the age distribution in the sample mirrored that in the population so that the number of fish in each age-class was e^{-Z} times the number in the preceding year-class. Finally, it was assumed that the lengths of fish at a given age were normally distributed, and table 22 of Pearson (1932) was used to estimate standard deviations of lengths at age from the ranges and sample sizes. The estimated values of VA are given in Table 1.

In fitting the model the population mean values were taken from the above growth curve for bonito, i.e. $\mu(l_\infty) = 76.87$ cm, $\mu(k) = 0.6215 \cdot yr^{-1}$, and $\mu(t_0) = -0.410$ yr. A trial and error process was then employed. Trial values of the other model parameters ($\sigma(l_\infty)$, $\sigma(k)$, $\sigma(t_0)$, ρ, and Z) were chosen, a population of 5000 fish was simulated, and values of VA, VL, and GD were calculated for the simulated population. The process was repeated in an attempt to find parameters which produced growth variability (VA and VL) similar to that estimated above.

This proved impossible. Parameters that produced appropriate values of VA inevitably resulted in values of VL that were much too small. Parameters that produced $VL_1 = 35\%$ always resulted in $VA_1 > 20\%$. Although the above estimation procedure for VA may not give very precise estimates, it is hard to believe it would be this far out. Model values of GD were always positive.

The parameters that gave the best fit to VA alone (ignoring the fit to VL) were $\sigma(l_\infty) = 2$ cm, $\sigma(k) = 0.05 \cdot yr^{-1}$, $\sigma(t_0)$ = 0 yr, and $\rho = 0.9$ (the mortality, Z, does not affect VA or GA). Model estimates for these parameters (together with an assumed value of $Z = 1 \cdot yr^{-1}$) are given in Table 1. Good agreement was obtained between the estimated ("data") and fitted ("model") values of VA. The growth rate difference was found to increase with age, both in relative terms (GD increasing from 3% at age 1 to 196% at age 6) and absolutely (GL − GA increasing from 0.4 to 1.3 cm).

Two reasons may be given for this increase with age. The first has to do with the mortality-dependent balance between numbers of young (= fast-growing) and old (= slow-growing) fish of a given length (see comment on mortality in above example). As the length increases, the range of possible ages at that length increases and mortality causes the balance to swing further in favour of the fast-growing fish. The second reason affects only the older ages. For example, GL_5 is an average growth rate over all fish of length 74.2 cm (Table 1). This excludes all those slow-growers with $l_\infty < 74.2$. By contrast, GA_5 is an average over all fish of age 5, fast- and slow-growers included, and so should be expected to be $<GL_5$. This contrast will be even greater between GL_6 and VL_6.

In order to understand how the model parameters affect VA, VL, and GD, further simulations were carried out starting with the parameters of Table 1 and successively changing one parameter at a time (Table 2). From these it may be seen that GD increases with increasing mortality (Z) and increasing growth variability (VA, VL).

Growth variability is affected in different ways by the model parameters. $\sigma(l_\infty)$ affects VA, VL, and GD across all age-classes whereas $\sigma(k)$ affects these quantities more in the younger fish and has a stronger effect on VA than on VL (compared with $\sigma(l_\infty)$). The only effect of $\sigma(t_0)$ is to change VA for the first year or two. Decreasing ρ decreases VA, VL, and GD.

A few simulations were carried out with some modifications to the model. When a logistic equation was used in place of the von Bertalanffy curve, it was found that (very small) negative

TABLE 1. Comparison between direct ("data") and model estimates of mean length, growth variability, and growth rates for Pacific bonito (*Sarda chiliensis*). Model parameters were chosen to give best fit for mean length and VA. See text for details.

			Growth variability							
	Mean length (cm)		VA (%)		VL (%)		Annu. growth (cm)		Growth diff. GD (%)	
Age (yr)	Model	Data	Model	Data	Model	Data	GL	GA	Model	Data
1	44.9	44.9	7.5	7.0	11	35	15.2	14.8	3	−37
2	59.7	59.7	5.9	6.1	16	35	8.5	7.9	7	−15
3	67.6	67.6	4.8	5.2	23	—	5.0	4.3	17	—
4	71.9	71.9	4.1	4.4	31	—	3.2	2.3	40	—
5	74.2	74.2	3.5	3.5	38	—	2.4	1.2	92	—
6	75.4	75.4	3.2	2.7	42	—	2.0	0.7	196	—

TABLE 2. Effect of model parameters on growth variability (VA, VL) and the difference between growth rates at age and at length (GD). The first line shows the model parameters as for Table 1, with the corresponding values of VA, VL, and GD at ages 1 and 4. In succeeding lines, all model parameters except the one shown are the same as in the first line.

Model parameters					Growth variability					
Mortality	SD			Corr.	VA (%)		VL (%)		Growth diff. GD (%)	
Z	l_∞	k	t_0	ρ	1	4	1	4	1	4
1.0	2	0.05	0.0	0.9	7	4	11	31	3	40
0.5					7	4	11	35	2	23
2.0					7	4	11	26	4	62
	1				6	3	8	22	2	17
	4				10	7	17	39	5	93
		0.025			5	3	9	31	1	31
		0.1			12	6	16	32	7	58
			0.1		9	4	11	32	3	38
				0.0	6	3	8	30	2	25
				−0.9	3	1	3	27	0	10

values of GD could be obtained but only with very low mortalities. The introduction of different mortalities above and below a fixed "recruitment" length was tried but did not seem likely to lead to a markedly better fit to the bonito data. It was not possible to reproduce a decrease in GD with increasing age, as was observed above for flounder.

Discussion

This paper has shown that the comparison of growth information from age–length and tagging data is equivalent to comparing mean growth rates at age, GA, to mean growth rates at length, GL, and that these are not, in general, equal. It is instructive to ask why this difference is not common knowledge. More important is the question of how much the growth rates may differ.

That the difference is not generally recognised may be because growth models, at least in the fisheries literature, tend to be interpreted rather loosely. For example, Sainsbury (1980, p. 241) remarked that many authors do not distinguish between equations describing individual growth and those for growth in a population. This difference is crucial because the conventional models, (1) and (2), are equivalent when applied to individuals but not for populations. Also, some authors appear to confuse maximum mean length at age and maximum (individual) length, and so are (unnecessarily) troubled to find that their estimated l_∞ is less than the maximum observed length (e.g. Campbell and Collins 1975, p. 187; Ralston and Miyamoto 1983, p. 531).

It must not be thought that this difference is a matter of mathematical inadequacy. A change of parameterization, equation, or method of estimation will not make the problem go away. It arises out of a fundamental difference between the growth information in the two types of data: age-based for age-length data and length-based for tagging data.

One inference from this is that Kirkwood's (1983) attempt to estimate growth parameters from a combination of age–length and tagging data was, although a commendable idea, logically flawed because he did not use a growth model which incorporated both the age- and length-based aspects of growth. How serious this flaw is depends on how much we can expect GD to differ from zero in a real population.

The above attempts, by direct estimation and modelling, to answer this question were inconclusive. The direct estimates suggest that GD may be significantly different from zero in either direction and that the difference decreases in magnitude with age. In contrast, the modelling suggests that GD cannot be large and negative and that it increases rapidly with increasing age.

Of course the direct estimates may be unreliable because of inaccuracies in ageing, the influence of tagging on growth, or any of the factors mentioned in the last paragraph of the introduction. This too could explain why the model used was unable to fit the data for either species. However, we must also ask if the model itself is adequate.

Since it is the existence of growth variability that allows GD to differ from zero, it is important to consider how variability is incorporated into this (and other) models. Elsewhere (Francis 1988a), I reviewed models of growth variability in the context of tagging data. Of the models considered there, all those that are also applicable to age–length data are similar to the model used here in that each fish is assumed to grow deterministically according to its own set of parameters. That is, all growth variability is assumed to be endogenous. Given the known dependence of fish growth rates on environmental conditions such as temperature and food availability (Weatherly 1972), it seems important to consider models in which growth variability is, at least partly, exogenous.

I know of no such published model, but N. G. Dow (Fisheries and Wildlife Service, Box 114 Queenscliff, Vic. 3225, Australia, pers. comm.) has devised an ingenious model in which all growth variability is exogenous. When the von Bertalanffy equation is used in this model and mortality is assumed constant (or, more generally, dependent on age alone), it may be shown that GD is always zero, regardless of the level of mortality. This occurs because, in this model, fish that grew faster than average in the past will not necessarily continue to do so in the future. A correlation between past and future growth rates is a feature of the endogenous model.

Although Dow's model may come no closer than the above model to reproducing the estimated values of GD for bonito and flounder, it demonstrates clearly that there is more than one way of modelling variability. Furthermore, the way this is done may have a dramatic effect on GD. Perhaps a third way can be found which will reproduce the values of GD estimated above for bonito and flounder.

As is often the case when models are used to investigate biological problems, a conclusion to be drawn from the modelling here is that the currently available models are inadequate; in particular, more flexibility is required in the description of growth variability. A mixture of endogenous (genetic) and exogenous (environmental) variability should be modelled and the effect of mortality on mean age at length should be recognized. In fitting the model, both age-based (VA) and length-based (VL) measures of variability should be considered. Finding typical values of variability to use with a model is also a problem — the two estimates of VL used here are the only published values I know of.

There appears to be no clear indication in the literature as to whether growth variability within a population is driven mostly by environmental or genetic factors. There is abundant evidence that different populations of the same species of fish will grow at markedly different rates because of different environmental conditions (e.g. Weatherley 1972, fig. 2.5 and 2.6). However, the question of whether individuals within a population experience sufficiently different environmental conditions to explain observed differences in growth is a very different matter, and this is the question of interest here. As to genetic input, Weatherley (1972, p. 128) concluded that there was little evidence to prove that fish inherit more than an upper limit to the size which they may attain. It is unlikely that this difficult issue will be resolved theoretically in the near future; the test of adequacy for any model must remain its ability to mimic empirical data.

A type of data set which may be useful, both for direct estimation of GD and in suggesting realistic ways to model growth variability, is lengths at age, back-calculated from scales or otoliths (e.g. see Hile 1970). Such data provide a growth history for each fish and may be treated either as conventional age–length data or as length–increment data akin to that from tagging. A successful model for these data would need to account for both annual variations in growth rates and, where necessary, Lee's phenomenon.

For the meanwhile, researchers should refrain from using a comparison of growth parameters derived from the two types of data as a means of validation of one or the other. Comparisons that have already been made should be reconsidered. For example, one may query the conclusion of Ikenouye (1969) that *Beryx splendens* produce two translucent bands per year in the otolith because growth rates estimated from tagging data were much higher than those from age–length data assuming one band per year. If the von Bertalanffy equation is to be used, then the new parameters given here will avoid the ambiguity in the conventional parameters and provide a better description of growth.

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Growth Rates and Growth Efficiencies in Larvae and Juveniles of *Rutilus rutilus* and Other Cyprinid Species: Effects of Temperature and Food in the Laboratory and in the Field

W. Wieser and H. Forstner

Institut für Zoologie, Universität Innsbruck, Technikerstrasse 25, A-6020 Innsbruck, Austria

F. Schiemer

Institut für Zoologie, Universität Wien, Althanstrasse 14, A-1090 Wien, Austria

and W. Mark

Institut für Zoologie, Universität Innsbruck, Technikerstrasse 25, A-6020 Innsbruck, Austria

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Growth rates were determined in four 0+ class populations of roach (*Rutilus rutilus*): two from warm backwaters of the Danube and two from cold-water lakes. Larval growth was also determined in the laboratory for *R. rutilus*, *Leuciscus cephalus*, and *Alburnus alburnus* at 15, 20, and 25°C. Q_{10} values of growth rates were low (1.29–1.67) between 20 and 25°C but were high (3.9) between 15 and 20°C. Net growth efficiency of the larvae of *R. rutilus* ranged from 68.6 to 71.9% at 15°C and from 72.3 to 73.5% at 20°C. A comparison of temperature-corrected relative growth rates in the four populations of roach revealed significant differences between the two warmwater and the two cold-water populations. Growth of warmwater populations was fastest right after hatching and then declined in a fairly regular way. Growth of cold-water populations was slow after hatching but increased later. These differences reflect interactions between temperature and food availability in the two types of water bodies. The sudden increase in growth rate in the population from the coldest lake can be correlated with a change in gut contents which in turn reflects the improved ability of the juvenile fish for catching zooplankton.

Le taux de croissance a été mesuré chez quatre populations de gardon (*Rutilus rutilus*) de classe d'âge 0+ ; deux des populations provenaient d'eaux mortes tièdes du Danube, les deux autres de lacs d'eau froide. La croissance des larves a été mesurée au laboratoire chez *R. rutilus*, *Leuciscus cephalus* et *Alburnus alburnus* à 15, 20 et 25°C. Les valeurs Q_{10} des taux de croissance étaient faibles entre 20 et 25°C (1,29–1,67), mais élevées entre 15 et 20°C (3,9). L'efficacité nette de la croissance des larves de *R. rutilus* se tenait entre 68,6 et 71,9 % à 15°C, et entre 72,3 et 73,5 % à 20°C. Une comparaison des taux de croissance relatifs après correction pour la température, chez les quatre populations de gardon, a montré des différences significatives entre les deux populations d'eau tiède et les deux populations d'eau froide. Chez les populations d'eau tiède, la croissance était la plus rapide dès l'éclosion et elle ralentissait assez régulièrement par la suite. Chez les populations d'eau froide, la croissance était lente après l'éclosion, mais augmentait par la suite. Ces différences montrent qu'il y a des interactions entre la température et la disponibilité des aliments dans ces deux types de plans d'eau. L'augmentation subite de la croissance dans les populations des lacs d'eau froide peut être mise en corrélation avec les changements observés dans le contenu stomacal; cela témoignerait de l'habileté supérieure des juvéniles dans la capture de zooplancton.

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The interactions between growth and developmental processes of fishes during the first weeks after hatching have received little attention. In nature, there is a premium on fast growth for larvae because mortality is highest in those stages (Hjort 1914; Laurence 1975; Ehrlich and Muszynski 1982; Wieser 1985). However, a series of developmental changes that involves the differentiation and reorganization of the feeding apparatus gills, muscle, and sense organs takes place during the larval period (Blaxter 1986; El-Fiky et al. 1987; El-Fiky and Wieser 1988). Many of these developments are reflected in changes of feeding behaviour and food composition of larval and juvenile fish (Hammer 1985; Mark et al. 1987). The question arises to which extent the requirement for fast growth is influenced by changes in structure and function of the growing fish. In addition, growth is decisively influenced by the specific conditions of temperature and food availability in the environment (Brett 1979; Keast 1985). Thus, complex interactions may be expected between developmental processes and environmental influences which can be analyzed only by comparing growth curves derived from natural populations with the responses of laboratory populations of the same species to controlled changes of temperature and food conditions.

Here we report on such an investigation in which the growth rates of four populations of roach (*Rutilus rutilus*), two from a warm, eutrophic water body in East Austria and two from cold, oligotrophic lakes in West Austria (Schiemer 1985; Wieser 1986a; Rheinberger et al. 1987), were compared with the growth responses of roach and other cyprinid species raised in the laboratory at different temperatures and fed *Artemia* nauplii ad libitum. In conjunction with previous measurements of oxygen consumption (Wieser and Forstner 1986), this comparison leads to a better understanding of the factors responsible for the variability of the rates and efficiencies of growth of larval cyprinids in the field.

TABLE 1. Major variables of the growth of *Rutilus rutilus* after hatching in two cold-water lakes (Piburg, Seefeld) and in a warm backwater (Stopfenreuth, 1984 and 1985).

Date (d/mo)	Age (d)	n	T (°C)	Fresh weight (mg)	
				$\bar{x}$	SD
Piburger See, 1984					
25/5	4	6	13.1	1.4	0.1
30/5	11	4	13.2	1.7	0.1
6/6	18	6	15.3	2.1	0.3
14/6	26	10	18.2	3.7	0.2
27/6	39	2	18.8	11.0	0.3
3/7	45	12	17.1	14.9	2.2
9/7	51	23	22.1	23.2	6.3
18/7	60	54	19.5	48.9	9.9
26/7	68	19	19.4	94.0	17.7
5/8	78	2	20.8	169.7	20.7
14/8	87	8	19.2	326.8	41.8
29/8	102	9	19.5	639.9	120.9
Stopfenreuth, 1984					
6/6	16	14	19.0	12.1	2.2
4/7	44	66	16.7	159.3	32.1
12/7	52	486	21.4	216.9	56.1
24/7	64	209	22.6	367.7	128.8
2/8	73	126	20.8	519.8	174.7
13/8	84	64	19.7	556.8	200.1
20/8	91	26	20.8	827.3	234.9
5/9	107	35	21.7	1073.1	191.0
Seefelder See, 1985					
12/6	7	17	13.6	2.4	0.4
18/6	13	32	13.6	3.2	0.5
21/6	16	31	14.3	3.7	0.5
26/6	21	29	15.2	4.0	0.8
28/6	23	30	16.0	4.4	1.1
3/7	28	37	17.8	5.1	0.8
8/7	33	21	18.7	6.5	1.2
12/7	37	22	18.9	6.9	1.5
15/7	40	30	19.7	9.4	2.1
19/7	44	40	20.8	27.1	9.0
23/7	48	43	22.4	31.1	12.3
26/7	51	36	20.8	41.4	25.4
30/7	55	61	20.3	56.2	19.7
14/8	70	49	17.5	88.8	28.1
22/8	78	41	18.7	129.6	44.2
30/8	86	31	13.6	165.2	42.5
5/9	92	21	16.8	170.0	36.0
Stopfenreuth, 1985					
31/5	20	50	20.1	8.3	2.6
5/6	25	50	22.1	18.7	5.4
18/6	38	50	17.2	42.8	15.8
27/6	47	75	19.3	103.1	28.3
3/7	53	200	18.1	159.3	37.6
10/7	60	197	19.2	198.0	43.7
17/7	67	242	20.4	273.3	82.2
23/7	73	202	21.5	348.8	123.5
30/7	80	200	20.3	383.6	105.5
15/8	96	46	22.1	651.7	291.1
23/8	104	100	21.5	801.3	223.5
4/9	116	64	19.1	1139.0	365.1
1/10	143	26	12.7	1016.7	433.0

Material and Methods

Larval and juvenile roach were collected by means of scoop nets or fry traps (Rheinberger et al. 1987) from two oligotrophic cold lakes in Tirol (the Piburger See in 1984 and the Seefelder See in 1985; see Wieser 1986a) and from an eutrophic warm backwater of the Danube in East Austria (near Stopfenreuth in 1984 and 1985; see Schiemer 1985). The fish were put for a few hours into water-filled containers to void their guts and then fixed in 4% formaldehyde. Specimens were briefly blotted on tissue paper and weighed. Data on the four populations are summarized in Table 1. Other specimens were dissected shortly after they had been caught and the food composition in the gut was analyzed as described by Mark et al. (1987). Water samples were taken in Seefelder See simultaneously with the fish samples and the composition and density of the plankton determined. Adult roach (abbreviation Rr), chub (*Leuciscus cephalus*, abbreviation Lc), and bleak (*Alburnus alburnus*, abbreviation Aa) were taken from lakes in Tirol and Upper Austria (Mondsee) to the laboratory and maintained in running water 2–3° warmer than the natural environment. Ovulation and spermatogenesis was induced by injection of carp pituitary in a 0.6% NaCl solution. The eggs were fertilized and left to develop attached to glass plates in running water at 20°C. After the larvae had started to accept food (2–3 d after hatching in Rr and Lc; approximately 8 d after hatching in Aa), they were fed *Artemia* nauplii ad libitum by means of an automatic dispenser which ensured a continuous and homogeneous flow of nauplii. On day 9, one group of Lc was transferred to 25°C, and on day 13, two groups of Rr were transferred to 15 and 25°C. One group of Aa remained at 20°C; another one was transferred to 25°C on day 8. In this way it was possible to determine Q_{10} values during the periods of fastest growth. Weights were determined at intervals of from 3 to 7 d. Each measurement was based on 10 subsamples, each consisting of from 10 specimens early in the study to 3 secimens towards the end of the study.

The rates of growth were expressed either by plotting the logarithms of fresh weight against age (days after hatching) and calculating linear regressions through the data points or by fitting higher (up to 5) order polynomials to the points (Pollard

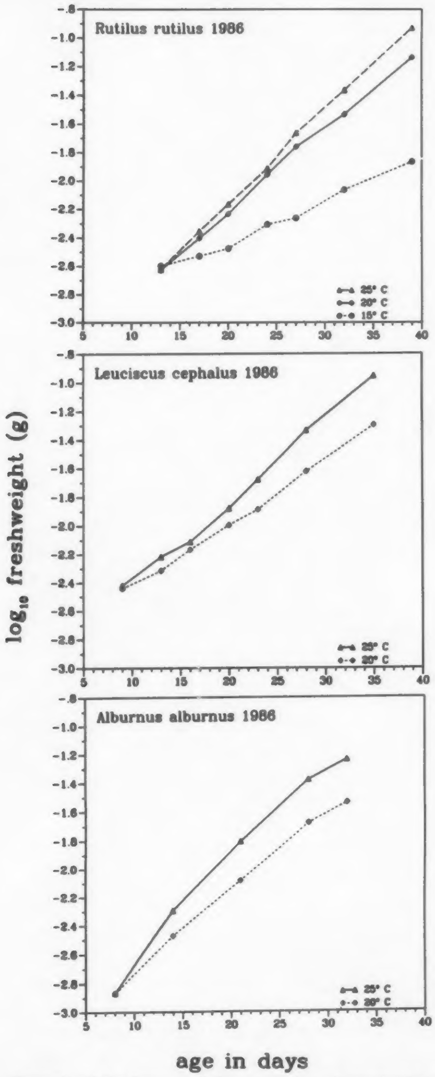

FIG. 1. Growth of the larvae of three species of cyprinids at two or three experimental temperatures during the first 5 wk after hatching. $\log_{10}$ values of fresh weights are plotted against age (days after hatching), the symbols representing the mean values of weight samples as described under Material and Methods.

1977). Significance of the polynomial terms was tested using ANOVA.

Results

Laboratory Experiments

Growth and temperature

In the cases of Rr and Lc the relationship between the logarithm of fresh weight and age is best described by linear regressions (Fig. 1). This suggests a function of the form $w_1 = w_0 \cdot e^{Gt}$ *where* w_0 and w_1 are fresh weights (fw, grams) on the first and last day of each temperature experiment, respectively, G is the growth coefficient, and t is time (days) after hatching.

TABLE 2. Statistical parameters and Q_{10} values of growth experiments at different temperatures with larvae of three species of cyprinids fed *Artemia* nauplii ad libitum. G = growth exponent; G_r = relative growth rate (% fw·d⁻¹); n = number of samples.

		G				
	T (°C)	$\bar{x}$ (SD)	r^2	G_r	n	Q_{10}
R. rutilus	15	0.067 (0.003)	0.987	6.9	7	3.92
	20	0.132 (0.003)	0.997	14.2	7	1.29
	25	0.151 (0.002)	0.999	16.3	7	
L. cephalus	20	0.102 (0.003)	0.997	10.8	7	1.67
	25	0.132 (0.004)	0.994	14.2	7	
A. alburnus	20	0.128 (0.005)	0.995	13.7	5	1.46
	25	0.156 (0.012)	0.903	16.9	5	

Only in Aa at 25°C is a more complex relationship indicated, but even there the rate of growth is closely approximated by a linear regression. The slopes of the regression lines represent the growth coefficient G from which the relative growth rate (G_r, percent fresh weight per day) is calculated according to $G_r = e^{Gt} - 1$.

The effect of temperature on the rate of growth was large in the range 15–20°C ($Q_{10} = 3.9$, measured only in Rr) but fairly small in the range 20–25°C ($Q_{10} = 1.29$–1.67) (Table 2). Furthermore, at a given temperature only insignificant differences exist between the growth rates of the three species.

Changes in growth rate

In order to establish the temperature relationship of the rate of growth, it suffices to plot the logarithms of body weight against age for different temperatures and to calculate linear regressions through the data points. However, such a procedure ignores short-term changes of the rate of growth. A more complex representation of the growth process, allowing much better resolution of the time course of growth in the developing fish, is achieved by fitting higher order polynomials to all data points. The first derivative of such a curve may be called the true rate profile of growth. In Fig. 2, fifth-order polynomials were fitted to the growth data of two populations of Rr and to one population of Lc at 20°C, including the period of retarded growth during the first days after the beginning of feeding which was omitted for the calculation of the temperature quotients of growth rate. Despite some differences between the three groups of fish tested, their rate profiles have a number of features in common. Growth is slow after the onset of feeding in all groups, the relative rates of growth ranging from 3 to 6%·d⁻¹. Growth accelerates afterwards to a first maximum at 17–25 d after hatching and then decelerates again. Beyond the age of 40 d, corresponding to a fresh body weight of approximately 80 mg, the growth curves become unreliable because *Artemia* nauplii do not constitute an optimal diet for fish of this size.

Growth efficiency

In a previous investigation (Wieser and Forstner 1986) the routine rate of oxygen consumption at 15 and 20°C has been determined in Rr and other cyprinids from the time of hatching up to a body mass of approximately 1 g. The mass relationship of oxygen consumption ($\dot{M}_{O_2}$, micromoles per gram per hour) can be described by two exponential functions:

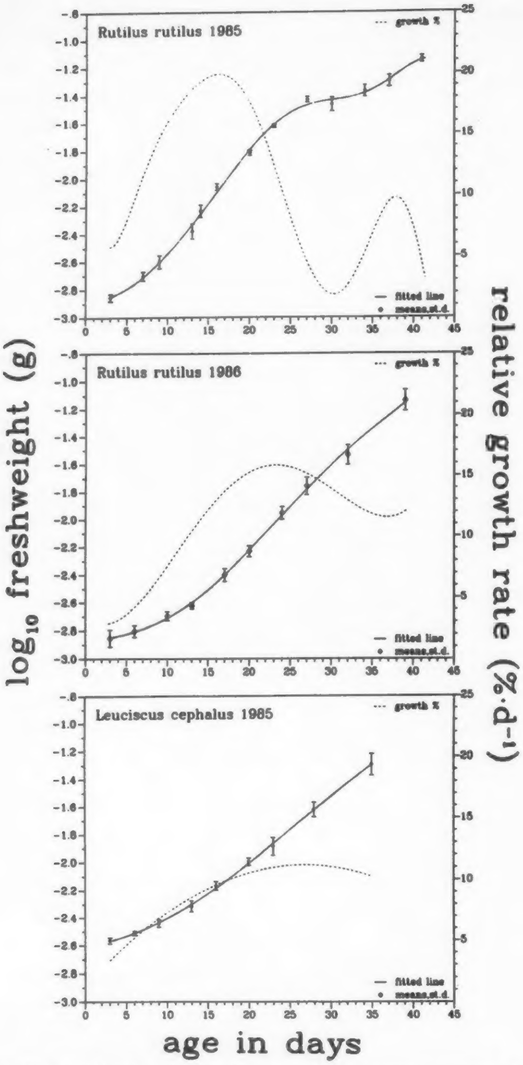

FIG. 2. Growth and relative growth rate of three groups, representing two species, of cyprinids fed *Artemia* nauplii ad libitum in the laboratory at 20°C. The logarithms of fresh weight (solid curve) and the relative growth rate (broken curve) are plotted against days after hatching. The growth curves are the result of fitting fifth-order polynomials to the measured values (of which means and standard deviations are indicated).

$$15°\text{C}: \dot{M}_{O_2} = e^{(2.62-2.10M)} + 3.33$$
$$20°\text{C}: \dot{M}_{O_2} = e^{(2.96-2.67M)} + 10.0$$

where M is fresh body weight (grams). Assuming an oxicaloric equivalent of 450 kJ·mol$(O_2)^{-1}$ (Wieser 1986b), weight-dependent aerobic power (R, mW·g^{-1}) may be calculated by the functions

$$15°\text{C}: R = 0.125e^{(2.62-2.10M)} + 0.42$$
$$20°\text{C}: R = 0.125e^{(2.96-2.67M)} + 1.25.$$

At the same time the relative rate of growth, G_r, can be expressed in terms of power by using a caloric equivalent of body mass. According to Hinterleitner et al. (1987), up to an age of 100 d, roach larvae contain approximately 80% water, 11% protein, and 8% fat. By using the equivalents for protein and fat given by Gnaiger and Bitterlich (1984), we arrive at an overall caloric equivalent of 5.8 kJ·g fw^{-1}. This permits the calculation of the net efficiency of growth, $[P/(P + R)]\cdot 100$, K_2 in the terminology of Ivlev (1945), where P represents the caloric equivalent of the relative rate of growth and R the routine rate of oxygen consumption of individual fish. Laboratory-bred Rr at 15 and 20°C convert *Artemia* nauplii into cyprinid body substance with high efficiency (Table 3). The efficiency increases slightly as the fish grow because the weight-specific rate of oxygen consumption decreases (Wieser and Forstner 1986) whereas the relative rate of growth remains constant during this early phase of growth. Another aspect emerging from Table 3 is the near temperature independence of growth efficiency between 15 and 20°C. This is due to the fact that the temperature relationships of the two rate processes, growth and metabolism, are nearly identical.

TABLE 3. Rates of growth (P), routine rate of metabolism (R), and net growth efficiency (K_2) in laboratory-bred *Rutilus rutilus* during the period of fastest growth (13–39 d after hatching), determined at 15 and 20°C. Units of P and R are mW; K_2 corresponds to $[P/(P+R)]\cdot 100$; growth rates are those given in Table 1; respiration rates are from Wieser and Forstner (1986).

Body mass		15°C			20°C		
mg	J	P	R	K_2	P	R	K_2
2.5	14.5	0.0116	0.0053	68.6	0.0238	0.0091	72.3
5	29	0.0232	0.0106	68.6	0.0476	0.0182	72.3
10	58	0.0464	0.0210	68.8	0.0952	0.0360	72.6
20	116	0.0928	0.0414	69.2	0.1940	0.0710	73.2
50	290	0.2320	0.0983	70.2	0.4760	0.1680	73.9
100	580	0.4640	0.1810	71.9	0.9520	0.3097	75.5

Field Data

Growth and growth rates of four populations of R. rutilus

Variations in growth rate are predominantly due to temperature and food availability. The effects of temperature can be compensated by extrapolating the rates measured at a given temperature to a common constant temperature, using Q_{10} values established in the laboratory. We assumed that the instantaneous rate of growth on a given sampling date reflects the average field temperature measured on this and the preceding sampling date. By means of the Q_{10} values for Rr established for the range 15–25°C in the laboratory (Table 2), we extrapolated the measured rates to 20°C, thus arriving at "20°C-corrected" body weights. The procedure is exemplified by Fig. 3a–3d, referring to the population from Seefelder See.

On the basis of the growth curve the relative rates of growth (percent fresh weight per day) can be calculated (Fig. 4). Unfortunately, because of flooding a long interval separated the first two sampling dates in the population from Stopfenreuth in 1984. If it is assumed that in that year the distribution of growth rates was similar to that of the following year, a clear difference emerges in the pattern of growth between the two warmwater and the two cold-water populations. In the warmwater populations, growth is rapid (up to 20%·d^{-1}) and then declines with time and body size in a fairly regular way. In the cold-water populations, growth right after hatching is much slower but either speeds up drastically (Seefeld, up to 30%·d^{-1}) or remains

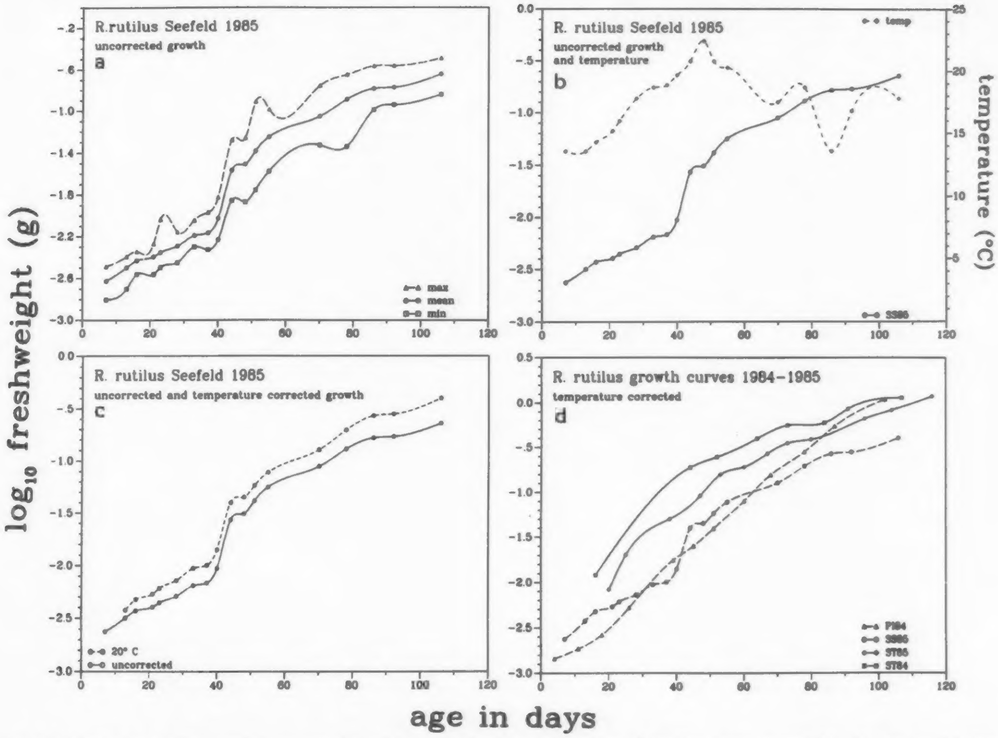

FIG. 3. Calculation of temperature-corrected growth curves for four populations of *Rutilus rutilus* exemplified by the population from Seefeld, 1985. Growth is represented by the logarithms of fresh weight plotted against age (days after hatching) (which in Seefeld took place on about June 5). (a) Means, maxima, and minima of actual weight measurements; (b) means of weight measurements (solid line) and temperatures (broken line) at collecting site; (c) means of weight measurements, uncorrected (solid line) and corrected for growth at 20°C (broken line); (d) temperature-corrected growth curves for the four populations of Rr: Piburger See (PI 1984), Seefelder See (SS 1985), and Stopfenreuth (ST 1984 and 1985). Spline interpolations were used for the graphic representations of the growth curves.

relatively high throughout the summer (Piburg). These differences may reflect differences in food supply which in the cold lakes is still very poor when Rr hatches (second half of May to first week of June). Because the temperature effects on growth have been subtracted, the remaining fluctuations of the rates must be predominantly due to fluctuations of food availability. This, in turn, reflects the more favourable conditions at the time of hatching in Stopfenreuth (Table 1).

Relationships between growth rate and food composition

In the Seefelder See the most conspicuous change in growth rate occurred between July 5 and August 2, when the larvae increased from 9.5 to 20 mm in total length and the relative growth rate varied between about 3 and 30%·d^{-1} (Fig. 4). During this time the qualitative and quantitative composition of the gut contents of the larvae also changed rather drastically (Fig. 5). As summarized in Table 4 the major break occurred between July 12 and 19 when the larvae had reached a total length of approximately 10 mm. Between these two sampling dates, phytoplankton disappeared almost completely from the food ingested, the volume of the food objects in the gut increased about fivefold from approximately 50 to 250 nL, and the proportion of crustacean plankton (mainly consisting of the cladocerans *Pleuroxus truncatus*, *Ceriodaphnia pulchella*, and *Alona* spp.) in the gut increased from about 50 to 85% of the gut contents.

Discussion

We have used basic information on the energetics of growth in young cyprinids maintained under controlled conditions in the laboratory to assess the patterns of growth of the same species in nature. The temperature experiments implied that the step from about 15 to 20°C acts as a stimulus to speed up growth in nature. The Q_{10} value over this range was about twice as large as that over the range 20–25°C. It is significant that in our lakes, cyprinids spend the first months after hatching in the shallow littoral where the temperature usually fluctuates around 20°C (Fig. 3; Rheinberger et al. 1987). By extrapolating the growth rates of all field populations to a common temperature of 20°C, we were able to minimize the effect of temperature on growth rate. Since at constant temperature and with ad libitum feeding the early growth of roach can be described by a logistic curve (Tong 1986), the rates of growth must decline with age. Irregularities in this decline seen in natural populations are probably due to irregularities of food supply. Some examples of changes in growth rates in nature are given for the Seefelder See population (Fig. 4) in which growth was suppressed during the first weeks after hatching but accelerated during one week

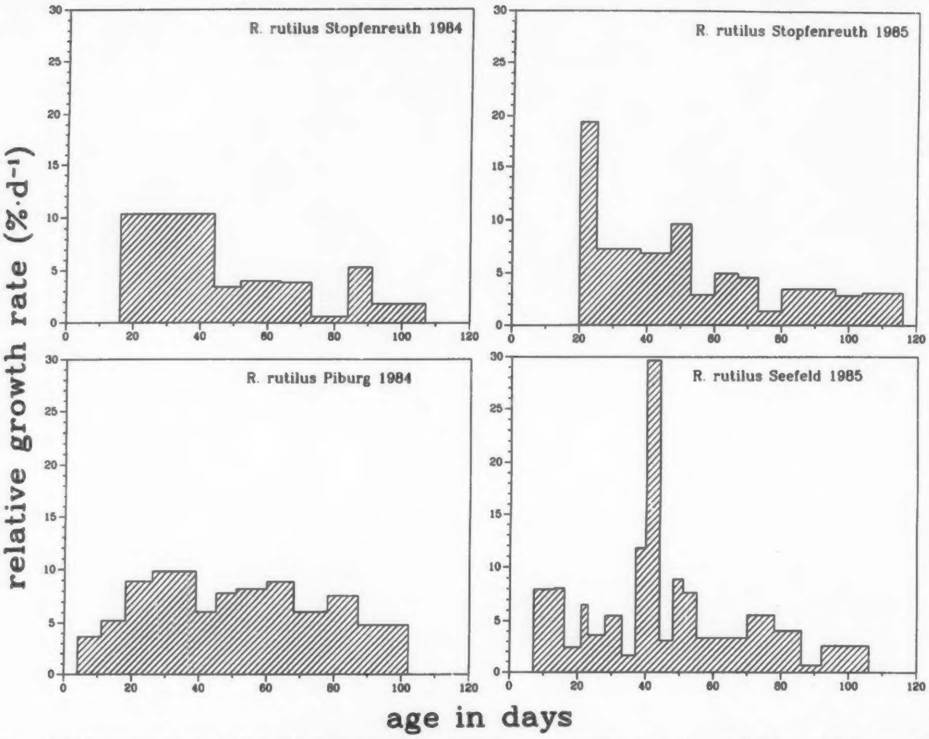

FIG . 4. Histograms representing relative growth rates between two sampling dates for populations of Rr from four Austrian water bodies (see Material and Methods).

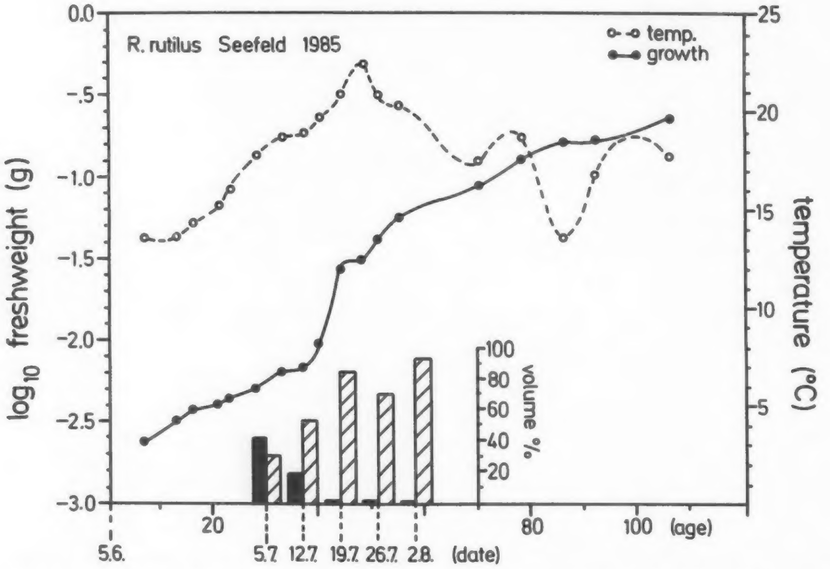

FIG. 5. Comparison of the growth curve of Rr from Seefelder See, 1985 (see Fig. 3b), with changes in food composition between July 5 and August 2. The histogram indicates changes in the density (as volume percent of gut contents) of two major food components, phytoplankton (solid columns) and crustacean plankton (hatched columns), during a period when the mean body mass of the population increased dramatically.

TABLE 4. Distribution of major food components in the guts of roach larvae and in lake water sampled simultaneously with the fish in Seefelder See, 1985. The lake water values represent averages of three to seven 1-L samples. The composition of food objects in the gut is given in percent of total gut contents, based on volume determinations of major food components.

Date (d/mo)	5/7	12/7	19/7	26/7	2/8
Mean length of fish (mm)	9.5	10	12	14	20
Number of specimens analyzed	10	17	10	12	10
% volume of gut contents					
Phytoplankton	42.8	19.6	0.3	1.5	0.3
Rotifers	1.0	1.5	0.1	1.2	0.1
Crustaceans	31.0	52.9	84.9	70.4	93.6
Chironomid larvae	24.7	25.8	12.4	13.8	1.8
Other insects	—	—	2.4	13.1	4.2
Total volume of food particles in gut (nL·fish^{-1})	63.1	49.6	233	259	908
Density of plankton in lake water (no.·L^{-1})					
Rotifers	249	233	253	434	78
Crustaceans	124	41	21	78	23

in July. Growth rates up to 30%·d^{-1} were measured during this period which is more than was observed in larval cyprinids fed *Artemia* nauplii in the laboratory (up to 21%·d^{-1}; see Fig. 3b and Dabrowski 1984) and higher than maximum rates reported for other natural populations of roach (Grigorash et al. 1972; Tong 1986; Rheinberger et al. 1987). The sudden acceleration of growth in the Seefeld population of Rr may be due either to a new and rich source of food in the lake or to the larvae having reached a stage when they become more efficient in catching and handling prey. Up to July 12 the larvae swallowed large amounts of phytoplankton which they are unable to digest, a dietary characteristic of the early larvae of roach and other cyprinids (Hammer 1985; Mark et al. 1987). This feature may be taken as an indicator of the undirected and erratic swimming movements of the larvae up to the time when the swimming muscles and sense organs are fully differentiated (Blaxter 1986; El-Fiky et al. 1987; El-Fiky and Wieser 1988).

Once the process of differentiation has been completed the juvenile fish become more efficient in locating and catching prey which in the Seefelder population is reflected by the disappearance of phytoplankton from the gut contents, by the increase in the proportion of crustacean plankton ingested, and, above all, by the dramatic increase in the volume of food in the gut. Because during the period of observation the average density of prey organisms in lake water at the site where the fish were caught did not vary markedly (Table 4) the change in growth rate occurrng around July 12 appears to be due to developmental rather than to environmental events. A conspicuous change in growth rate also occurred at around 20 d in groups of cyprinids fed ad libitum and maintained at 20°C in the laboratory. In this case it can be shown that the change in growth rate coincides with the differentiation of the adult-type red and white muscle fibres from the larval "red layer" and "central mass" of fibres, respectively (El-Fiky et al. 1987; El-Fiky and Wieser 1988). It seems that this step represents a characteristic developmental "stanza" (Ricker 1979) in the lives of the larvae that is of significance not only for the development of muscular functions but also for the way energy is partitioned in the body.

In laboratory experiments the "net efficiency of growth" (K_2 according to Ivlev 1945), is of the order of 70–75% and nearly temperature independent between 15 and 20°C (Table 3). Equally high values of conversion efficiency have been reported in larvae and juveniles of other species of fish (Ivlev 1939; Kinne 1960; Brett 1983). However, in nature the rate of growth may vary by an order of magnitude within a short period. This may imply an equally great variability of the efficiency of food conversion, or a rate of metabolism that varies along with the rate of growth, leading to invariant efficiencies. From what we know about energy partitioning in animals the latter is to be expected (Case 1978; Hogendoorn 1983; Jobling 1985; Wieser 1985, 1986b), but surprises cannot be excluded.

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Growth Rates and Protein Turnover in Atlantic Cod, *Gadus morhua*

D. F. Houlihan

Department of Zoology, University of Aberdeen, Aberdeen, Scotland

S. J. Hall

Marine Laboratory, Victoria Road, Aberdeen, Scotland

and C. Gray and B. S. Noble

Department of Zoology, University of Aberdeen, Aberdeen, Scotland

Houlihan, D. F., S. J. Hall, C. Gray, and B. S. Noble. 1988. Growth rates and protein turnover in Atlantic cod, *Gadus morhua*. Can. J. Fish. Aquat. Sci. 45: 951–964.

Atlantic cod, *Gadus morhua*, were maintained on different ration levels or starved to produce a variety of growth rates. The in vivo rates of protein synthesis and degradation were determined for the whole fish and various tissues. As ration level, and hence growth rates, increased, both whole-animal protein synthesis and degradation rates increased linearly; growth occurred because of the preponderence of synthesis over degradation. On average, a 300-g cod growing at $1.0\%\cdot d^{-1}$ synthesised 1.25 g of protein with 0.4 g of this protein remaining as growth. The proportion of total protein synthesis which was retained as growth increased with increasing growth rate; at a maximum growth rate of $2\%\cdot d^{-1}$, over 40% of the protein synthesised was retained as growth. The ranking of the tissues in terms of fractional rates of protein synthesis was liver > gills > intestine > spleen > ventricle > stomach > gonads > white muscle. The white muscle, gills, liver, stomach, spleen, and ventricle all showed similar patterns of increased protein synthesis with increased growth rate. The white muscle has the highest efficiency of retention of protein and accounts for 40% of the total protein accretion per day. In starving fish there was a constant level of protein synthesis, irrespective of the rate of weight loss. However, degradation rates increased in the whole animal and in white muscle as the rate of weight loss increased.

On a nourri des morues de l'Atlantique (*Gadus morhua*) de différentes rations ou on les a privées de nourriture afin de générer divers taux de croissance. On a ensuite déterminé les taux de synthèse et de dégradation de protéines *in vivo* chez les poissons entiers et dans divers tissus. On a observé une augmentation linéaire des taux de synthèse et de dégradation de protéines chez les poissons entiers en fonction d'une augmentation des niveaux de ration et donc des taux de croissance; la croissance a eu lieu à cause d'une prépondérance de la synthèse sur la dégradation. En moyenne, une morue de 300 g grossissant à un taux de $1,0~\%\cdot d^{-1}$ a synthétisé 1,25 g de protéines dont 0,4 g ont servi à la croissance. La proportion de la synthèse totale de protéines servant à la croissance a augmenté en fonction d'une augmentation du taux de croissance; à un taux de croissance maximum de $2~\%\cdot d^{-1}$, plus de 40 % des protéines synthétisées ont servi à la croissance. L'ordonnance des tissus en terme de taux partiels de synthèse des protéines est la suivante : foie > ouïes > intestin > rate > ventricule > estomac > gonades > muscle blanc. Le muscle blanc, les ouïes, le foie, l'estomac, la rate et le ventricule ont montré des régimes semblables d'augmentation de la synthèse des protéines en fonction d'une augmentation du taux de croissance. Le muscle blanc a montré l'efficacité la plus élevée de rétention des protéines et est responsable de 40 % de l'accroissement total quoditien de protéines. Chez les poissons non nourris, on a observé un niveau constant de synthèse de protéines indépendamment du taux de perte de poids. Toutefois, les taux de dégradation ont augmenté chez les poissons entiers et dans le muscle blanc en fonction d'une augmentation du taux de perte de poids.

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The relationship between food intake and growth rate has been well documented for Atlantic cod, *Gadus morhua* (Edwards et al. 1972; Jones and Hislop 1978; Hawkins et al. 1985). To date, however, few data are available on the rates of protein synthesis and degradation which underlie growth, with the exception of in vitro sutdies of protein synthesis (Lied et al. 1983; Lied and Rosenlund 1984). This study investigates rates of protein synthesis and degradation in cod maintained on various feeding levels ranging from starvation to satiation.

In growing fish a close relationship between rates of growth and protein synthesis is to be expected (Smith and Thorpe 1976; Smith 1981; Rosenlund et al. 1984; Houlihan et al. 1986).

However, protein accretion (growth) requires levels of protein synthesis in excess of the amount deposited (Millward et al. 1975; Laurent et al. 1978). Studies with intact mammals suggest that protein synthesis rates exceed deposition rates by a factor of from 1.5 to 2 (Reeds et al. 1981; Reeds and Harris 1981). The difference between synthesis and growth results from protein degradation. The first part of the present study concentrates on the levels of protein synthesised in relation to the levels of protein retained as growth in the whole bodies of growing and starving cod.

Many fish species may be expected to encounter periods when food supply is inadequate for maintenance and growth. For cod this is especially likely during winter when benthic productivity is low (Hawkins et al. 1985). Fish must therefore possess mechanisms for storing components of the diet in the tissues when meals are being absorbed, for later use during times of food scarcity and during the reproductive phase(s) of the life cycle when reserves are diverted into reproductive tissues. Skeletal muscle is a likely candidate as the major site for protein storage; it is the largest tissue in the body (40–60% of total live weight) and has been shown to be the tissue in which protein synthesis rates are most sensitive to starvation (Smith 1981). In addition, white muscle has further advantages as a store owing to the very high efficiency of retention of synthesised protein as growth that this tissue exhibits (65–80%) (Smith 1981; Houlihan et al. 1986; Houlihan and Laurent 1987).

Loss of weight during starvation results from an excess of degradation over synthesis. It appears, however, that tissues vary in their response to lack of food. For example, in rainbow trout, *Salmo gairdneri*, there were no significant changes in protein synthetic rates in the liver and gill after starvation for 15 d whereas, in contrast, protein synthesis in muscle declined over the same period with a concomitant increase in the rate of degradation (Smith 1981). Similarly, Loughna and Goldspink (1984) showed that loss of body weight is accompanied by a decrease in the rates of protein synthesis in both red and white muscle and, at least initially, an increase in protein degradation in the white muscle. A decrease in the rate of protein synthesis in white muscle during starvation has also been found in an in vitro study of cod polyribosomes (Lied et al. 1982). It appears, therefore, that the positive relationship between synthesis and degradation observed in growing tissues becomes decoupled in white muscle during starvation.

To investigate the mechanisms involved in the stimulation of growth through feeding, reliable methods for in vivo measurement of protein synthesis and degradation are required. An important factor in the recent advances in the measurement of protein synthesis in vivo has been the introduction of theoretically sound and experimentally reproducible methods. Garlick et al. (1980) described the use of a single high-dose injection of ^{3}H-phenylalanine for the measurement of protein synthesis in various tissues of the rat. A number of studies have applied these methods to fish (e.g. Haschemeyer 1983; Pocrnjic et al. 1983; Houlihan et al. 1986). In the present study the phenylalanine free pool flooding method has been used to measure the protein synthesis rates of whole bodies and various tissues of feeding and starving cod. We have also estimated the growth rates of the tissues and used these values to estimate the rate of breakdown, since net gain of protein (growth) is the difference between synthesis and degradation (Millward et al. 1975).

TABLE 1. Diet composition and energy content. Each mean (±SE) value for the composition is given as a percentage of the total weight and the energy content is in J·mg ash-free dry weight^{-1}.

Protein	40.69 ± 1.86
Carbohydrate	4.28 ± 0.35
Ash	30.89 ± 2.01
Water	21.47 ± 0.58
Energy content	23.27 ± 4.6

Materials and Methods

Feeding experiments were conducted from July to November 1985 at the Marine Laboratory, Aberdeen, with juvenile Atlantic cod trawled from the Firth of Clyde. In these experiments the first month served as an acclimation period during which stressed or infected fish could be replaced. Throughout the experiment, animals were maintained in individual 35 × 65 cm (70 L) aquaria supplied with running seawater maintained at 10 ± 0.5°C. Stock fish for replacement of unhealthy fish during the acclimation period were kept in a 1.5 × 1 m holding tank supplied by the same seawater system.

Feeding and Growth

A total of 24 fish were used in the experiment. During the first 2 wk of the acclimation period, fish were fed ad libitum and the quantity of food eaten by each individual was recorded; based upon these data, fish were assigned to one of three groups (eight fish per group) and within each group all eight fish were assigned a ration level (ranging between 1.0 and 4.0% body weight·d^{-1}). Fish were fed every second day throughout the experiment, with the exception of a fortnightly weighing when individual fish were starved for 24 h before weighing and were left a further 24 h before the commencement of feeding. To limit stress effects while weighing fish, the water volume in the aquaria was reduced and individuals were anaesthetised by the addition of MS 222 (10 000 ppm) before removal. After weighing, the fish were returned to fresh seawater in their own aquarium.

At each feeding, individuals were presented, one pellet at a time, with a preweighed portion of a manufactured food, the total amount available at any one session being determined by the ration level for that individual. A pellet was only offered after the previous one had been eaten: on occasions when an individual failed to eat all of the allotted ration the remainder was reweighed to give an accurate measure of food consumption.

The diet was manufactured from powdered, freeze-dried natural prey, indentical to that used in studies of growth in juvenile cod by Hawkins et al. (1985). This diet (Table 1) was chosen because it provided prey items in the proportion found in the stomachs of wild fish. Furthermore, it permitted direct comparison with previous growth experiments.

During the acclimation period all fish were kept under a photoperiod equivalent to that for midsummer in Scotland (latitude 57°33′00″). After the acclimation period, the photoperiod of two groups of eight fish each was shifted, one forward relative to that which prevailed on 2 October 1985 and the other back to the photoperiod for 10 April 1985. For these two treatments the photoperiod was advanced, on a weekly basis, from these starting points to follow the natural changes in day length from autumn to winter and spring to summer, respectively.

The photoperiod manipulations described above formed part of a further study to be dealt with elsewhere. Unfortunately, six fish died during the experiment and are not included in this analysis. Fish mortalities were evenly spread between ration levels and did not affect the balance of the experiment.

Starvation and Weight Loss

Nine fish for the starvation experiment were transferred to the laboratory in April 1986, having been previously held without food for 2 wk at the Millport Marine Station, Isle of Cumbrae. Animals were weighed on arrival and held in 1.5 × 1 m aquarium at 10°C for a further 2 wk before reweighing.

Growth Rates of Fish and Tissues

Specific growth rates over the final 2 wk before the measurement of protein synthesis were calculated from the following equation (Ricker 1979):

$$\text{Growth rate } (\%\cdot\text{d}^{-1}) = \frac{(\log_e W_2 - \log_e W_1)}{t} \times 100$$

where W_1 is the initial weight (grams), W_2 is the final weight (grams), and t is the length of the growing period (days). It should be noted, however, that growth rates were monitored over the 3 mo preceding synthesis measurements.

To estimate the growth rates of the individual tissues in growing animals over the 2 wk preceding the protein synthesis determination, a series of dissections were performed on 33 cod trawled from the Firth of Clyde in November 1986. The fish ranged from 73 to 492 g. From these dissections the allometric relationship between total wet body weight and the weight of gills, ventricle, stomach, intestine, and white muscle were determined.

Dissections were performed in the following manner. A median ventral incision was made from the branchiostegal membrane to the posterior border of the body cavity. The visceral mass was then removed after cutting at the oesophagus and anus and the liver, spleen, pyloric caecae, stomach, and intestine were separated. The stomach was taken as being from the cut at the oesophagus to just above the pyloric sphincter, while the intestine was taken as being from just below the pylorus to the anus; food was removed from the gut before weighing. The ventricle was removed from the pericardial cavity by cutting at the atrial ventricular junction and just below the bulbus arteriosus. Gills were removed after making cuts at the top and bottom of the branchial arches (gill weight includes the arch). After removal of all the fins and the shoulder girdles, the white muscle was dissected by careful filleting from the spinal column as far onto the head as was possible. The remainder, including the fins, was taken as the skeleton although it should be noted that this includes the jaw musculature, eyes, and brain.

The allometry of the tissues was described using the power relationship

$$Y = aX^b$$

where $Y =$ wet weight of the tissue (grams), a is the intercept, X is the total weight of the fish (grams), and b is the exponent; the initial and final weight of each tissue could then be predicted from the initial and final weight of each fish.

Using the above predictions and values for tissue protein content (milligrams per gram), determined from the experimental animals at the end of the experiment, total protein content of each tissue at the initial and final weight was calculated. To permit this calculation, it is assumed that tissue protein content determined at the end of the experiment was the same 14 d earlier. From the difference in total tissue protein over the 2 wk immediately preceding death, specific growth rates of the tissues were calculated as described above for whole fish.

Protein loss calculations for starved animals were performed in an identical manner to that described above, using tissue allometry regressions obtained by dissection of cod starved for 2 wk. Although these regressions were used to predict tissue weights of experimental animals after both 2 and 4 wk of starvation, we do not feel that this introduces significant errors.

Rate of Protein Synthesis

Protein synthesis rates were determined for the feeding and starved fish. The starved fish were also used to determine the time course of free pool flooding.

The measurement of tissue protein synthesis rates from the incorporation of radioactive phenylalanine was based on the method of Garlick et al. (1980). On the day of injection, food was withheld and the animals were injected in the caudal vein without anaesthesia; all fish had been without food for approximately 24 h. This period was chosen to standardise treatments; food remained in the intestine at this time. The injection solution contained 150 mM L-phenylalanine and L-[2,6-^{3}H]phenylalanine (Amersham International) at 37 × 10^6 Bq·mL^{-1} (100 μCi·mL^{-1}) in Cortland ringer at pH 7.4 (specific radioactivity 1280 dpm·nmol^{-1}). The dose was 1.0 mL·100 g body weight^{-1} which represents from 8–16% of the blood volume (Jones and Randall 1978). This amount of phenylalanine should increase the free pool by some 12 times above the normal value if the amino acid is equally distributed to all the tissues. After the injection the fish were returned to aerated seawater at 10°C where they recovered immediately and rested quietly in covered containers. For the time course experiments the fish were killed 20, 40, and 60 min after the injection by a blow to the head and transection of the spinal cord. In all the other experiments the animals were killed 40 min after the injection. One-gram samples of gill, ventricle, stomach, intestine, liver, spleen, and white muscle were removed. White muscle samples were always taken from the dorsolateral aspect beneath the first and adipose fin; this is entirely within the mosaic region which is composed largely or entirely of glycolytic white fibres in the cod (Altringham and Johnston 1982). Dissections were performed on ice and were complete within 10 min of the death of the animals. Samples of the tissues were frozen in liquid nitrogen, stored at −70°C, and then processed as described below.

The total weight of each tissue was estimated using the regression equations described above, or by directly weighing at the time of dissection in the case of the liver and spleen. For the determination of the whole-body rate of protein synthesis of the growing animals the whole bodies (minus the samples described above) were freeze-dried, homogenised, and duplicate samples of the homogenate taken for analysis. For the starved animals the frozen whole bodies were homogenised directly in perchloric acid and duplicate samples of the homogenate taken for analysis.

For the determination of protein synthesis of the tissue samples, duplicate samples of approximately 100 mg of each tissue were homogenised in 2 mL of 2% perchloric acid (PCA). Further tissue treatment was as described by Houlihan et al. (1986).

Briefly the precipitate containing the protein was washed twice in 2% PCA, dissolved in NaOH, and protein determinations carried out on the resulting solutions by the method of Lowry et al. (1951) using bovine serum albumin as a standard. Protein-bound phenylalanine was obtained after hydrolysis of the protein in 6 N HCl. Specific radioactivity of the free pool phenylalanine (Sa) and the protein-bound phenylalanine (Sb) was then determined after the conversion of phenylalanine into β-phenylethylamine (PEA). The concentration of the latter was determined by fluorescence (Suzuki and Yagi 1976) against a standard curve of 0–15 nmol PEA.

Standard solutions of phenylalanine were used to quantify the recovery of PEA. Measurements of radioactivity were made in a Beckman scintillation counter using NE 265 liquid scintillant with a counting efficiency of from 30 to 40%.

The experimental results were obtained as Sa (dpm per nanomole) and Sb (dpm per nanomole). The fractional rate of protein synthesis, K_S, as a percentage of the protein mass synthesised per day was calculated as

$$k_s = \frac{\mathrm{Sb}(t)}{\mathrm{Sa}(t)} \times \frac{100}{t}$$

where Sb(t) is the protein-bound specific radioactivity at the experimental time t (usually 40 min) and Sa(t) is the free pool specific radioactivity at time t. For each fish the K_S value for each tissue was multiplied by the total amount of protein in the tissue to give the milligrams of protein synthesised per day.

Rates of protein degradation for each tissue were calculated as the difference between the rate of protein synthesis (percent per day) and the growth rate of the tissues (percent per day). The fractional rates of protein degradation were multiplied by the total weight of protein in the tissue at the time of death to give the milligrams of protein broken down per day. The mean results were compared using Student's t-test and the 5% level of confidence was used throughout. Regression analyses were compared by covariance analysis (Snedecor and Cochran 1976). Means ± SE are given throughout the text.

Results

Whole Fish

Growth rates

Specific growth rates over 3 mo were linearly related to ration (percent body weight per day). This relationship is described by the equation $Y = -0.575 + 1.13X$ ($n = 18$, $r^2 = 0.684$, $P < 0.001$) where Y = specific growth rate (percent body weight per day) and X = weight of food eaten (percent body weight per day). It should be noted that the high value for conversion efficiency (1.13) is a consequence of using an energy-dense pellet diet with low (21%) water content. The relationship between growth and ration size observed in this experiment could not be distinguished from that obtained by Hawkins et al. (1985) for cod maintained on an identical diet when the experiments were compared using covariance analysis (A. D. Hawkins, Marine Laboratory, Aberdeen, Scotland, pers. comm.). In the starved fish, weight loss was variable, possibly due to the intrinsic metabolism of the animals, the length of time since the last meal, and differences in the tissue storage products of the fish (Love 1980).

Time course of protein synthesis

The validity of the single high-dose injection depends upon three assumptions: (1) the presence of a high concentration of phenylalanine does not affect the rate of protein synthesis, (2) the labelled amino acid equilibrates rapidly with the intracellular pool, and (3) the specific activity of the free amino acid pool remains constant over the measurement period. With regard to the first assumption, Loughna and Goldspink (1985) have shown that in rainbow trout the injection of a high dose of phenylalanine does not affect the rate of protein synthesis in epaxial muscle.

The starved animals were used to determine whether the last two of these assumptions were correct. Figure 1a shows the recovery of L-phenylalanine determined by the fluorescence assay of β-phenylethylamine in various tissues at 20, 40, and 60 min after the caudal vein injection. For a 300-g fish the 450-μmol injection of phenylalanine should increase the free pool concentration in the tissues from a likely value of 130 nmol·g fresh weight^{-1} (Haschemeyer and Smith 1979) to 1500 nmol phenylalanine·g fresh weight^{-1} if it is equally distributed to all the tissues. In fact, 20 min after the injection, four tisues had free pool concentrations exceeding this value; the white muscle and the intestine had values slightly lower than the expected. Only the ventricle showed a significant fall in the concentration of the free phenylalanine after a further 40 min ($P < 0.05$). The white muscle samples showed highly stable free phenylalanine concentrations and there were no significant differences between white muscle samples taken from the anterior and posterior region.

The time dependency of the specific radioactivities in the free pools is illustrated in Fig. 1b. The values are slightly lower than that of the injection solution in the stomach and intestine 20 min after the injection. However, values for both tissues show no significant changes over time, and stability of the free pool specific radioactivity was therefore achieved.

The specific radioactivity of protein-bound phenylalanine showed linear increases over 40 min in all the tissues (Fig. 2). Four of the tissues showed linear increases over 60 min. The percentages of the total protein content synthesised per day (the fractional rate of protein synthesis, K_S, percent per day) were calculated for the three time intervals for each tissue; there were no significant differences between the three estimates.

Analysis of the free pool levels of phenylalanine in the fed animals showed that they also had flooding levels of this amino acid and that the free pool specific activity was similar to that of the injection solution.

From these results it was concluded that the fractional rates of protein synthesis could be accurately determined for all the tissues of fed and fasted fish by using the specific radioactivities of the free pool and the protein over the 40 min following an injection.

Whole-Body Growth, Synthesis, and Degradation

Whole body; feeding fish

The relationship between specific growth rate (K_G, percent per day, X) and the fraction of the total protein mass synthesised per day (K_S, percent per day, Y) for the whole-body analysis of the growing fish is described by the equation $Y = 1.47 + 1.16X$ ($n = 16$, $r^2 = 0.786$).[1] There is a significant correlation ($P < 0.001$) between the specific growth rate of the whole fish and the fractional rate of protein synthesis.

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[1] Complete set of tabular data is available, at a nominal charge, from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Canada K1A 0S2.

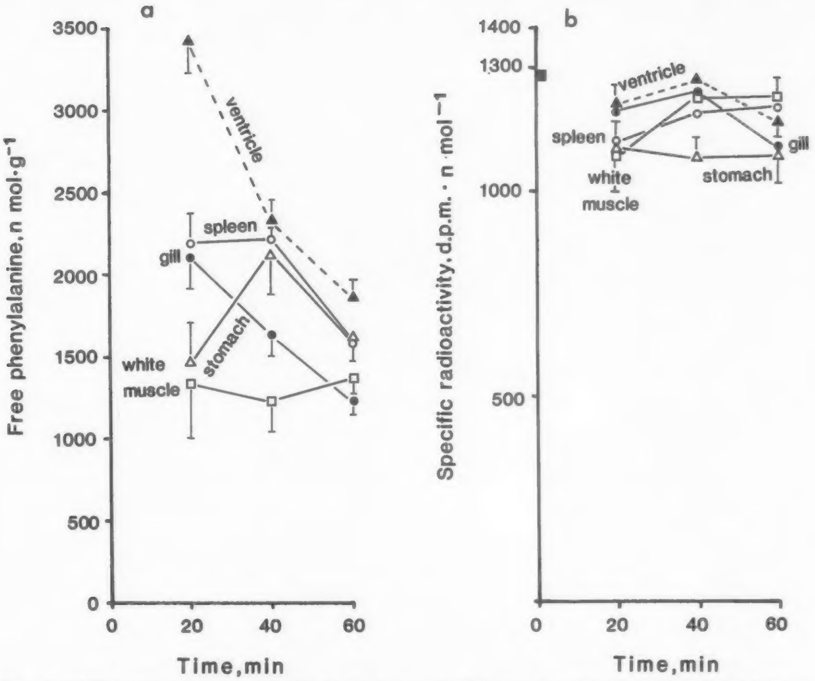

FIG. 1. (a) Recovery of L-phenylalanine in the free pools of tissues in cod held at 10°C. The fish (mean weight 344.28 ± 44.89 SE) received an injection of 150 mM phenylalanine and [^{3}H]phenylalanine at a dose of 1 mL·100 g body weight^{-1} at time zero. Each mean was calculated from nine tissues. (b) Specific radioactivity of free pool phenylalanine after the injection of [^{3}H]phenylalanine. Specific radioactivity of the injection solution is shown on the ordinate.

These data were also analysed after the application of a correction factor for variation in body size. A number of studies have shown a pronounced effect of body size, both on rates of growth (e.g. Elliott 1975; Brett 1979; Jobling 1983) and protein synthesis (Goldspink and Kelly 1984; Fauconneau 1985; Houlihan et al. 1986): increasing body size results in a decline in both weight-specific growth and fractional protein synthesis rates. Accordingly, the results obtained for each fish have been corrected to a "standard" 300-g animal using the equation $Y = aX^b$ where Y is the growth or synthesis rate (K_G or K_S, percent per day), X is the body weight (grams), and b is the correction exponent. For growth rate, a correction exponent of -0.441, obtained by Jobling (1983) from studies on cod, was used. Protein synthesis values were standardised using an exponent of -0.2 based upon the suggested relationship between protein synthesis rate and weight-specific oxygen consumption (Houlihan et al. 1986) and the exponent for weight-specific oxygen consumption found for cod (Soofiani and Priede 1985).

The corrected regression (Fig. 3a) has the values $Y = 1.42 + 1.68X$ ($n = 16$, $r^2 = 0.829$, $P < 0.001$). The coefficient of correlation (r^2) has increased after correcting for body size but the slope and evaluation of the regression equation are not significantly different from those obtained with the uncorrected data.

Using the corrected values, it can be seen that increased specific growth rate is accompanied by increased fractional synthesis rate. Taking a value of 1% growth per day for a 300-g animal, 3.1% of the total protein mass is being synthesised per day. This can be translated into the weight of protein synthesised per day by multiplying the fractional synthesis rate by the total protein content of the fish. Using the mean protein content of the growing fish (134.12 ± 5.52 mg protein·g fresh weight^{-1}), this gives 1.25 g of protein synthesised per day with 0.4 g being retained as growth. The calculated total amounts of protein synthesised per day for each fish varied between 1.9 and 10.3 times the amount of protein retained as growth.

The maximum specific growth rate recorded was 2%·d^{-1} for a fish fed ad libitum. The fractional rate of protein synthesis for a 300-g fish calculated from the regression equation described above was 4.78%·d^{-1} which is 3.37 times higher than that of a fish showing zero growth (the intercept value in the corrected regression described above). Thus the fractional synthesis rate for the whole fish had a greater than threefold expansibility (maximum rate divided by the minimum rate) whereas the growth rate showed a twofold increase.

The retention of protein in the growing fish can be expressed as a percentage of the daily rate of protein synthesis (K_G divided by K_S as a percentage); this can be termed the efficiency of protein retention. With increasing growth rate the efficiency of retention of synthesised protein increased (Fig. 4).

There was no significant correlation between the weight-specific rate of weight loss in the starving fish and the fractional synthesis rates using the uncorrected data. Indeed, inspection of these data (Fig. 3a) shows that the synthesis rates for the starving fish were constant and were similar to the levels shown by the slowest growing fish. There appears to be no data available on the effects of body size on the rate of weight loss during starvation in cod, thereby preventing the application of a cor-

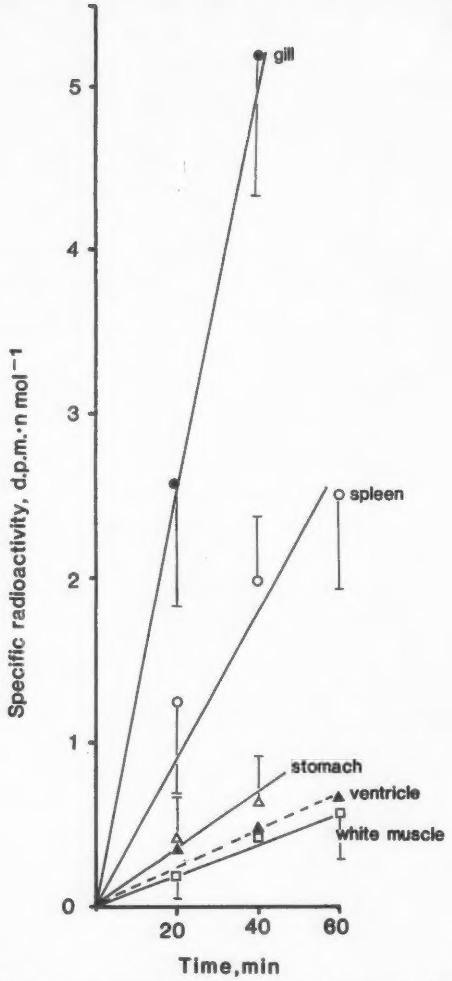

FIG. 2. Incorporation of labelled phenylalanine into proteins following a flooding dose at time zero. Other details are as in Fig. 1.

rection factor. Furthermore, the data presented here show no correlation between weight-specific weight loss and body size.

Inspection of absolute values for protein growth, synthesis, and degradation in starving fish showed that much of the protein which was degraded was, in fact, resynthesised rather than lost.[2] Indeed, for seven out of nine fish, synthesis exceeded net protein loss from the body.

Degradation rates

Fractional rates of protein degradation in the whole fish were calculated from the fractional synthesis rates minus the specific growth rates using the corrected values described above. There is a significant correlation between the specific growth rate and the fractional degradation rate for growing animals ($Y = 1.42 + 0.678X$, $n = 16$, $r^2 = 0.442$, $P < 0.01$).

In the starving animals the fractional degradation rates were found to increase with increasing weight loss. There is a significant correlation between the rate of weight loss and the rate of protein degradation ($Y = 0.825 - 1.59X$, $n = 9$, $r^2 = 0.552$, $P < 0.05$; Fig. 3b).

Tissue Growth, Synthesis, and Degradation

Tissue weight and protein content

Allometric equations describing the relationships between wet weight of each tissue and body weight are given in Table 2. In all cases there was a significant correlation between whole-body weight and the weight of the tissues ($P < 0.001$), and no slope differed from 1; in other words, for the tissue under consideration, the tissue mass remained as a constant proportion of the body mass in both growing and starving fish.

A comparison of the protein contents of the tissues revealed significant differences between the same tissues in fed and starved animals, with the starved animals having significantly higher levels of protein per gram fresh weight in three out of five cases (Table 3). However, the histories of these two groups of fish were not the same and such differences in tissue composition are likely to be a result of differences in nutritional histories prior to the laboratory studies.

Tissues: growth and synthesis for feeding and starving fish

The relationships between the weight-specific growth rate for each tissue (K_G, percent per day) and the fractional rate of protein synthesis per day (K_S, percent per day) for the tissues studied in the growing fish are shown in Table 4. For each tissue there was a significant correlation between the growth rate and the fractional rate of protein synthesis. For the white muscle there was no significant difference between K_S estimates from samples taken from different regions.

As with the analysis of the whole-fish results, we have applied correction factors for the effects of body size. Because the tissues are all growing isometrically and the effects of body size on tissue rates of protein synthesis have been shown to be similar in rainbow trout (Houlihan et al. 1986), we have used the same exponents in an allometric equation as those described above for the whole animal. With the exception of the intestine, the corrected values all show an improvement in the coefficient of determination (r^2) (Table 4).

Both the uncorrected and corrected regressions show that there is an increase in the fractional synthesis rate with increasing growth rate (Fig. 5). The slopes of the regression analyses are statistically different between the tissues. To clarify the ranking of the tissues, the fractional protein synthesis rates have been derived from the regression equations for a 300-g standard cod growing at various rates and the values of $1\%\cdot\text{day}^{-1}$ used to list the tissues (Table 5). The ratios between the maximum rate of synthesis and the minimum (the intercept values of the corrected regressions, Table 4) show that the white muscle has the greatest expansibility in fractional protein synthesis rates.

The total amounts of protein being synthesised per day in the growing animals gave the following ranking for total protein synthesised: whitle muscle > gill > intestine > stomach > ventricle.[3] The white muscle contributed 29.6 ± 6.3% of the total whole-body protein synthesis rates and 39.7 ± 3.6% of the whole-fish protein growth in growing animals.

The efficiencies of retention of protein in the tissues of the growing fish show that the efficiencies increased sharply with increasing growth rate and were highest in the white muscle (Fig. 6).

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[2] See footnote 1.

[3] See footnote 1.

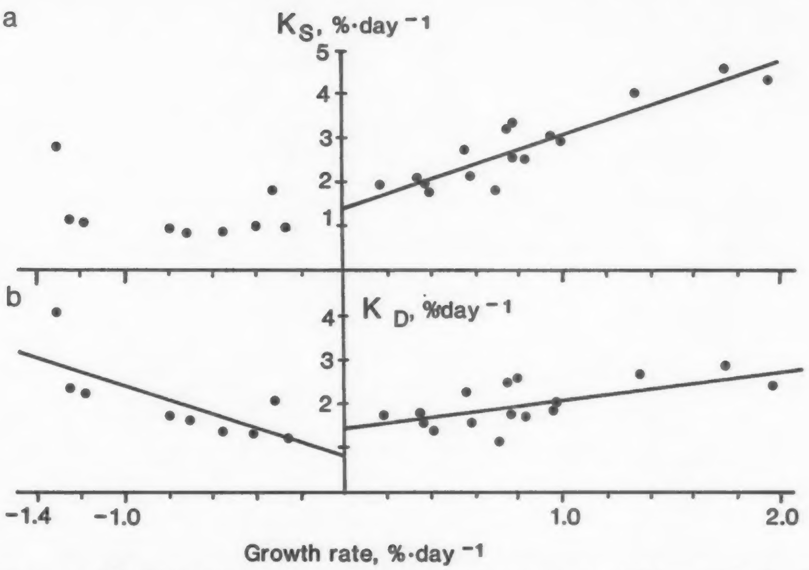

FIG. 3. (a) Relationships between whole animal growth rates and rates of weight loss and fractional rates of protein synthesis (percentage of the total protein mass synthesised per day, K_S). Growth rates are expressed as percentage growth per day for a standard 300-g cod and the fractional synthesis rates have also been corrected for a 300-g animal as described in the text. Rates of weight loss have not been corrected for body size. (b) Relationships between rates of weight loss and weight gain and fractional rates of protein degradation (percentage of the total protein mass degraded per day, K_D). Regression lines are taken from the regression equations described in the text.

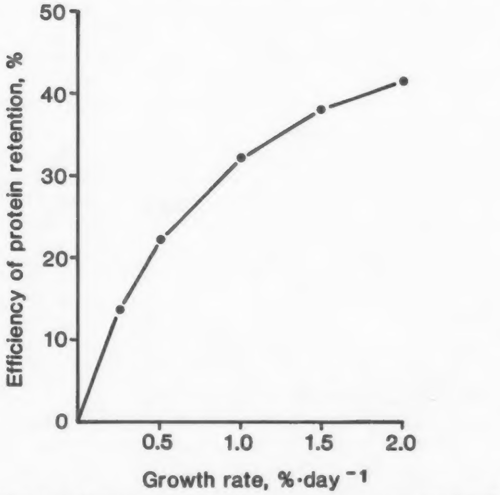

FIG. 4. Relationship between the whole-animal growth rate of fed fish and the efficiency of protein deposition. These data were calculated from the corrected growth and synthesis rates for a 300-g animal and the regression equation for growth/protein synthesis described in the text. The efficiency of protein deposition was calculated as percentage of protein synthesised retained as growth = (growth rate/protein synthesis rate) × 100.

TABLE 2. Tissue fresh weights (Y) in relation to total body fresh weight (X) for fed and starved cod using the allometric equation $Y = aX^b$. n is the number of determinations and r is the correlation coefficient.

Tissue	a	b+95% CL	n	r
Fed				
Gill	0.025	0.982 ± 0.075	33	0.978
Intestine	0.004	1.090 ± 0.168	33	0.921
Ventricle	0.003	0.977 ± 0.238	33	0.831
Stomach	0.012	1.040 ± 0.088	33	0.974
White muscle	0.632	0.977 ± 0.036	33	0.995
Starved				
Gill	0.049	0.884 ± 0.131	9	0.985
Intestine	0.018	0.838 ± 0.236	9	0.950
Ventricle	0.003	1.320 ± 0.359	9	0.952
Stomach	0.020	0.925 ± 0.191	9	0.971
White muscle	0.520	1.000 ± 0.061	9	0.997

TABLE 3. Tissue protein contents of fed and starved cod. Results (means ± SE) are in mg protein·g fresh weight⁻¹. $^*P<0.05$; $^{***}P<0.001$.

	Fed	Starved
Gill	71.96 ± 5.13	75.29 ± 3.18
Intestine	88.54 ± 5.26	111.88 ± 7.35*
Ventricle	104.64 ± 3.37	113.23 ± 4.77
Stomach	63.23 ± 6.06	123.40 ± 14.71***
White muscle	100.10 ± 3.38	120.16 ± 5.52***

There was no significant correlation between the specific rate of weight loss for the starving animals and the fractional rate of protein synthesis (Fig. 5). As with the whole-fish protein synthesis results, the tissue rates of synthesis for the starving animals appear similar to the lowest rates found in the slowest growing fish.

TABLE 4. Least squares linear regressions of growth rate (X) on the percentage of the total protein mass synthesised per day (Y) (the fractional rates of protein synthesis, K_s) using the equation $Y = a + bX$. Growth rates were calculated for the individual tissues using the equation $\log_e W_2 - \log_e W_1/t \times 100$ where W_1 and W_2 were the initial and final protein contents of each tissue over the growing period (t, days). The fractional rates of protein synthesis were determined over 40 min following the flooding dose of phenylalanine . The tissues are ranked in order of their fractional rates protein synthesis (see Table 5). The corrected values are those after the conversion of the values to a 300-g animal as described in the text. $^*P<0.05$; $^{**}P<0.01$; $^{***}P<0.001$.

Tissue	Uncorrected	Corrected
Gill	$Y = 4.32 + 5.82X$ $n = 12, r^2 = 0.34^*$	$Y = 4.44 + 5.61X$ $n = 12, r^2 = 0.37^*$
Intestine	$Y = 4.05 + 2.84X$ $n = 15, r^2 = 0.43^{**}$	$Y = 4.28 + 2.54X$ $n = 15, r^2 = 0.40^*$
Ventricle	$Y = 2.31 + 2.55X$ $n = 14, r^2 = 0.47^{**}$	$Y = 2.34 + 2.44X$ $n = 14, r^2 = 0.48^{**}$
Stomach	$Y = 1.62 + 2.57X$ $n = 13, r^2 = 0.37^*$	$Y = 1.59 + 2.60X$ $n = 13, r^2 = 0.40^*$
White muscle	$Y = 0.45 + 1.53X$ $n = 14, r^2 = 0.78^{**}$	$Y = 0.45 + 1.52X$ $n = 14, r^2 = 0.80^{**}$

In the starving animals the fractional synthesis rates of the gill, intestine, stomach and ventricle were usually greater than the fractional rates of weight loss and the calculated total amounts of protein being synthesised in these tissues were usually greater than the amount of protein being lost. Only in the white muscle was the rate of protein loss greater than the rate of protein synthesis. The white muscle protein loss contributed 65.7 ± 5.6% to the whole-body protein loss.

Fractional rates of protein degradation did not give significant correlations with growth rates in growing fish except for the white muscle (Fig. 7). For this tissue, growth rate (Y, percent per day) was related to degradation rate (X, percent per day) as $Y = 0.465 + 0.48X$ ($n = 16$, $r^2 = 0.22$, $P < 0.05$). Thus, as the white muscle grows, both fractional protein synthesis and degradation rates increase, with synthesis increasing more rapidly than degradation. The fractional degradation rates of the other tissues are increasing with increasing growth rate but generally yield correlation coefficients which are not significant. Only in the white muscle of the starving animals did the fractional rates of protein degradation give a significant correlation with specific weight loss ($Y = 0.677 - 0.906X$, $n = 9$, $r^2 = 0.89$, $P < 0.01$).

Incomplete data sets are available for some of the tissues. The liver showed a significant correlation between corrected synthesis rates and growth rates using the whole-animal corrected growth rate data ($Y = -2.56 + 17.1X$, $n = 12$, $r^2 = 0.71$, $P < 0.001$; Fig. 8). It was found during dissection of the initial group of feeding fish that liver weight was highly variable. It is not possible, therefore, to accurately predict the liver weight of individual fish at the beginning of the experiment to estimate the rate of protein accretion in the liver. Significant correlations between spleen and gonad fractional rates of protein synthesis and whole-animal growth rates were also found (spleen $Y = 1.76 + 2.5X$, $n = 14$, $r^2 = 0.51$, $P < 0.01$; gonad $Y = 0.41 + 2.31X$, $n = 13$, $r^2 = 0.56$, $P < 0.01$; Fig. 8). Unfortunately, however, accurate predictions of total tissue weights were once again not possible.

Discussion

Validity of Methods

The accuracy of the estimates of tissue growth or weight loss rates depends upon the accurate measurement of the growth rate of individual fish from whole-animal body weight and the accurate estimation of the weight of the tissues of individual fish at the beginning and end of the experimental period.

Fish growth was monitored over a 3-mo period but only the weight changes over the last 2 wk were used in the calculation of growth rates. The growth rates over the longer period showed a significant linear relationship ($P < 0.01$) with those found over the shorter experimental period.

Because of the need to estimate whole-body rates of protein synthesis the tissue weights at the end of the experimental period could not be directly determined. We are therefore reliant upon the analysis of the tissue weights from the dissections of a size range of fed and starved fish; regressions of whole-body weight and tissue weight were used to estimate rates of tissue protein loss or gain. Fortunately, for the bulk of the tissues investigated these regressions gave extremely good correlations (Table 2) and we therefore feel justified in using these in estimating growth rates. Although the tissue weight was estimated, the tissue protein contents (milligrams protein per gram fresh weight) were directly determined for each fish.

The results from the allometric analysis of the tissues are consistent with previous reports. The white muscle and ventricle in fish have both been found to be more or less a constant proportion of body size (Crile and Quiring 1940; Somero and Childress 1980; Houlihan et al. 1986). The gut mass is also close to a constant proportion of body size (Weatherley and Gill 1983).

The liver, spleen, and gonad failed to produce data with a significantly close relationship between body weight and tissue weight to permit reliable predictions. Accordingly, these tissues were excluded from the main analysis.

The comparison of protein syntheses rates between fed and starved fish used two separate groups of animals investigated at different times of the year. The variation in the rates of weight loss of the starved animals and absolute differences in tissue protein contents between fed and starved fish may be due to their previous feeding histories or other factors beyond our control. It is therefore even more remarkable that the synthesis rates of the starved fish were very close to the lowest rates measured for the feeding fish on the lowest ration.

The phenylalanine high-dose injection method seems to be effective for measuring protein synthesis rates in vivo. Two separate samples from the largest tissue in the body gave comparable results, suggesting that protein synthesis rates are similar throughout this tissue and indicating that previously experienced problems with measuring protein synthesis in the posterior region of the tail (Houlihan et al. 1986) may have been due to the lower dose of phenylalanine injected in that study.

As in previous studies of this kind (Goldspink and Kelly 1984; Houlihan et al. 1986), the degradation rate calculations are open to criticism, since it is assumed that rates of growth measured over weeks can be equated with rates of synthesis measured over minutes. There appears to be no solution to this problem until other methods of measuring protein degradation are available. An additional criticism lies in our assumption that, for the starving fish, the protein content of the tissues was the same from the middle to the end of the 4-wk starvation

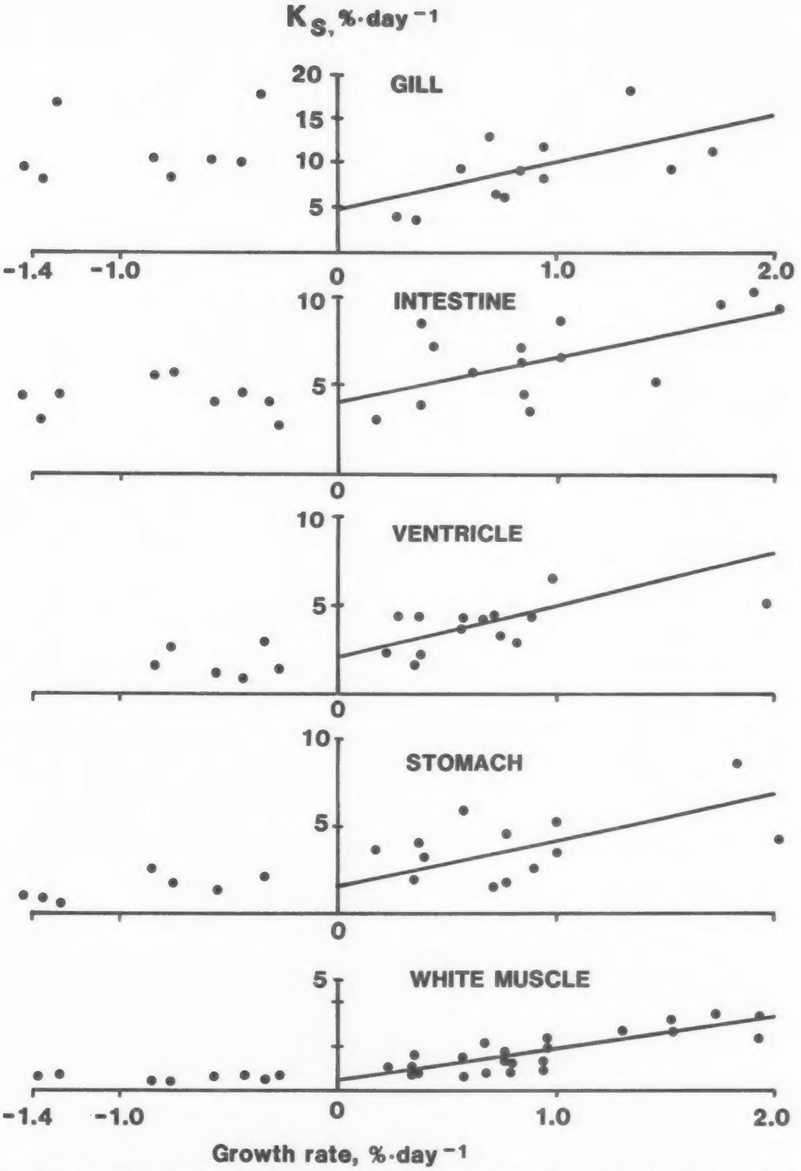

FIG. 5. Relationships between tissue-specific growth rates and rates of weight loss and fractional rates of protein synthesis (percentage of the total protein mass synthesised per day, K_s). Growth rates are expressed as percentage growth per day for a standard 300-g cod and the fractional synthesis rates have also been corrected for a 300-g animal as described in the text. Rates of weight loss have not been corrected for body size. Regression equations for significant correlations are given in Table 4 and in the text.

period, the period over which weight loss was measured. It is possible, however, that the protein content of tissues (milligrams per gram fresh weight) may have been changing over this period; Black and Love (1986), for example, have shown that protein is not sequestered until 82 d of starvation in cod.

Owing to the difficulties of obtaining sufficient numbers of uniformly sized animals, there was some variation in body size. As body weight itself has been shown to affect rates of protein synthesis, comparison of animals of different weights may best be carried out after a correction for body weight has been made. The value for the correction exponent is, however, open to question; −0.441 has been used here for growth rates (Jobling 1983) although it might be argued that −0.2 should be used for both growth rate and synthesis corrections. The methods are defensible on the basis that we have chosen a standard sized animal of 300 g whose weight is similar to that of the mean

TABLE 5. Fractional rates of protein synthesis calculated for a 300-g animal using the regression equations shown in Table 4. Rates are calculated for zero growth, 1%·d⁻¹, and 2%·d⁻¹. Ratios of maximum to minimum fractional synthesis rates are also shown.

Tissue	Growth rates (K_G) 0%·d⁻¹	1%·d⁻¹	2%·d⁻¹	Ratio maximum/minimum
Gill	4.44	10.05	15.66	3.53
Intestine	4.28	6.82	9.36	2.19
Ventricle	2.34	4.78	11.42	4.88
Stomach	1.59	4.19	6.79	4.27
White muscle	0.46	1.94	3.42	7.43

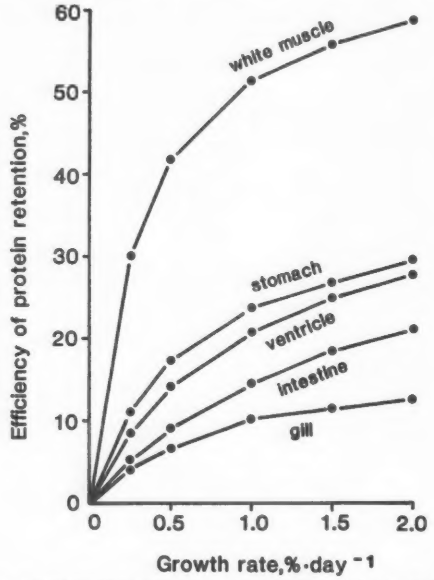

FIG. 6. Relationships between growth rates of fed fish and the efficiencies of protein deposition for the various tissues. The data was calculated from the corrected growth and synthesis rates for a 300-g animal shown in Table 4. The efficiency of protein deposition was calculated as percentage of protein synthesised retained as growth = (growth rate/protein synthesis rate) × 100.

weight of the growing animals (299 g) and the corrected regression equations are very similar to the uncorrected results. However, as we had no basis for correcting for weight differences in the starving group of animals, the greater variation in the fractional synthesis values for this group of animals may in part be explained on weight differences.

Rates of Protein Synthesis and Growth

Three major points are revealed from the measurements of protein synthesis rates and growth rates: (1) increasing growth rates brought about by increased rations are a result of increased protein synthesis rates, (2) the relationships between protein synthesis and growth rates are linear and have slopes greater than 1, and (3) increased rates of protein synthesis are accompanied by increased levels of efficiency of the retention of synthesised protein. These three points hold both for the whole-body and individual tissue analysis that we have performed.

As a corollary to these results on synthesis in the growing animals, we have shown that whole-body protein degradation rates also rise with increasing growth rates in a linear fashion. The linkage between synthesis and degradation has been shown for a number of tissues (Millward and Waterlow 1978; Goldspink and Kelly 1984; Houlihan et al. 1986; Houlihan and Laurent 1987); in the present case, high rates of synthesis are associated with high rates of degradation. Thus the coupling of synthesis and degradation found in growing rainbow trout (Houlihan et al. 1986) has also been found in cod in the present study.

In spite of the problems of comparing feeding and starving fish at different times of the year and with different nutritional histories, the results clearly show that over a 4-wk period, starvation does not reduce synthesis levels to zero. Rather, there is a constant rate of synthesis in all the tissues with some tissue synthesis rates ranked in the same order as for the growing fish. This indicates a necessity for a tissue such as the gills to continuously synthesise proteins at a high rate regardless of the nutritional intake.

Very generally, the whole-animal and white muscle synthesis rates show a plateau with weight loss in starving fish and a linear increase with increased ration. Interestingly, there is no indication of a further plateau at high ration levels from either growth (Soofiani and Hawkins 1985; data from this study) or protein synthesis values (data presented here). Degradation rates, on the other hand, show approximately a V-shaped response, with degradation rates increasing with increased rates of growth and increasing also with increased rates of weight loss in starving animals. Thus, in the latter case, protein degradation has become uncoupled from synthesis rates during starvation. A similar situation has been found in mammals; degradation rates have been found to increase linearly with growth rates in rat skeletal muscle (Millward et al. 1975) and degradation rates rise during starvation while synthesis rates fall (Millward and Waterlow 1978).

Calculation of the efficiency of the retention of synthesised protein shows that this rises rapidly with increasing growth rate which in turn is a reflection of increased ration. Fauconneau and Arnal (1985) have reported efficiencies of over 27% in rainbow trout. The increased efficiency with increased growth rate is due to the maintenance level of synthesis (the fractional synthesis rate during starvation) making a proportionately reduced contribution to the increasing synthesis rate. This improved efficiency of protein retention explains the often reported improved conversion efficiency with increased ration size in fish (Brett 1979).

Previously, estimates of the energetic costs of protein metabolism have been based only on measurements of protein deposition (growth), as these were the only data available. However, it has been acknowledged that energetic cost estimates based upon deposition would be underestimates (Jobling 1985), since growth is the result of the sum of synthesis and degradation.

The results presented here provide, for the first time, quantitative information on the rates of protein synthesis in whole fish and therefore permit an estimation of the energetic costs of protein deposition in fish. A 300-g cod contains 40.23 g of protein (using a mean protein content of 134.12 mg protein·g fresh weight⁻¹), and using the corrected data, at zero growth rate the fractional whole-animal synthesis rate is 1.42%·d⁻¹, i.e. 0.57 g protein·d⁻¹. The amount of energy required for protein synthesis is a matter of much debate; we have assumed a value of 50 mmol ATP·g protein⁻¹ (Reeds et al. 1985) although Jobling (1985) quoted a value of 100 mmol ATP·g protein⁻¹.

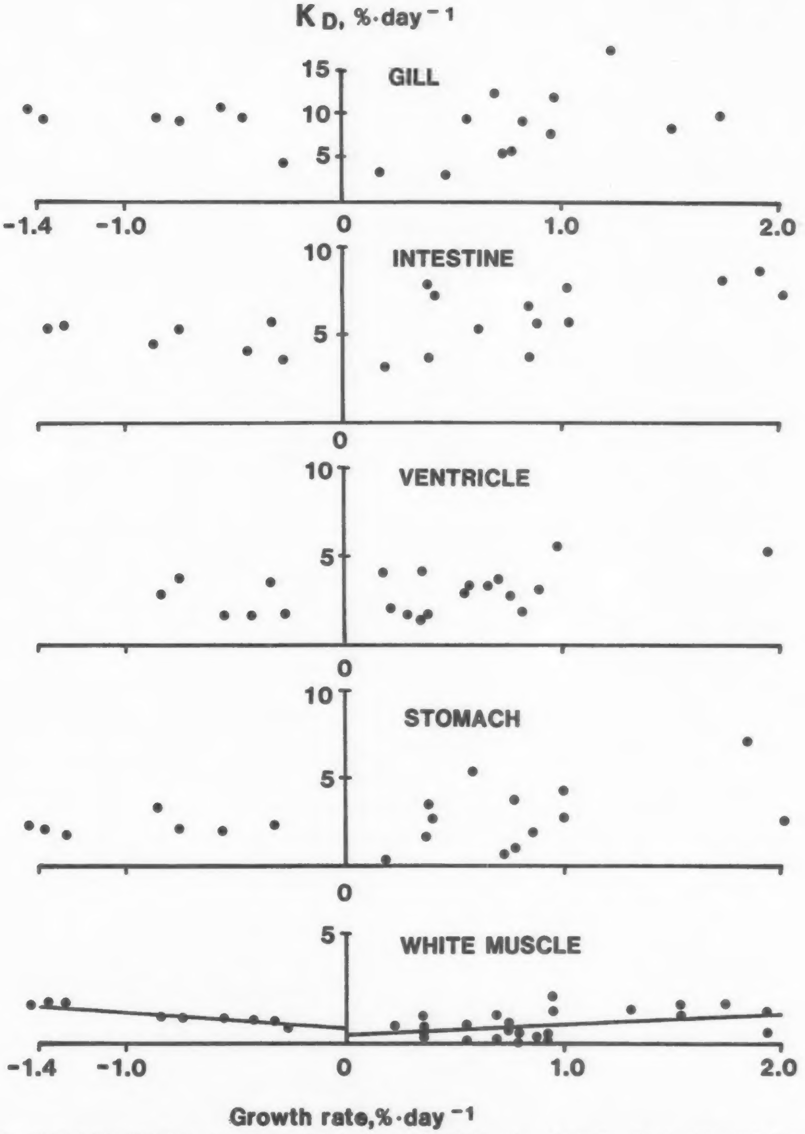

FIG. 7. Relationships between rates of weight loss and weight gain and fractional rates of protein degradation (percentage of the total protein mass degraded per day, K_D) for the tissues. The rates of weight gain have been calculated from the increase of protein in the tissues using the weight-specific growth rates and corrections made for body size described in the text. The fractional degradation rates were calculated for each fish and each tissue from the difference between the corrected fractional growth rates and the corrected fractional synthesis rates described in the text. Significant correlations between degradation rates and growth rates were only obtained for the white muscle. Regression equations are given in the text.

For a cod in the above example this is equivalent to 29 mmol ATP or 152 mg O_2·animal^{-1}·d^{-1}. Using the data from Soofiani and Priede (1985), a 188-g cod has a minimum respiration rate at 10°C of 101 mg O_2·kg^{-1}·h^{-1} (an inactive fish 2 d after feeding). Applying the body weight/metabolism correction described earlier, an estimate of oxygen consumption for a 300-g animal would be 644 mg O_2·animal^{-1}·d^{-1}. Thus the cost of protein synthesis in a starving fish represents 24% of the total oxygen consumption.

The maximum whole-body fractional rate of protein synthesis recorded here for growth at 2%·d^{-1} is 4.78%·d^{-1} which is equivalent to 1.92 g protein·300-g animal^{-1}·d^{-1} or 513 mg O_2·300-g animal^{-1}·d^{-1}. The maximum oxygen consumption of a 300-g cod which corresponds to the rate of oxygen consumption of fish fed to satiation (Soofiani and Hawkins 1985) is 1228 mg O_2·300-g animal^{-1}·d^{-1}. Thus, in such a fish, protein

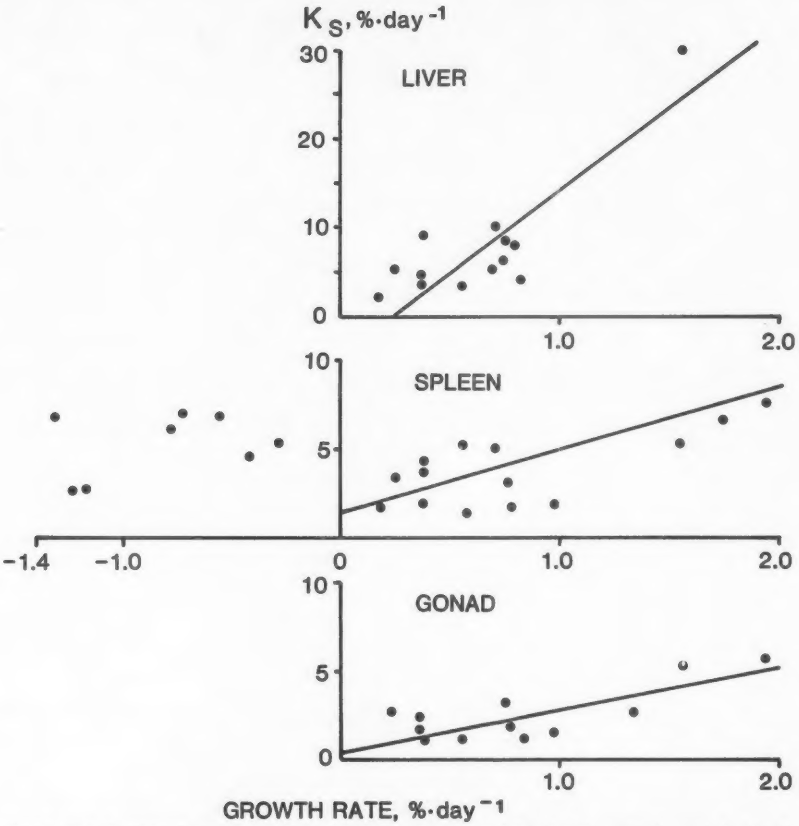

FIG. 8. Relationships between whole-animals growth rates and fractional synthesis rates for the liver, spleen, and gonad. The fractional synthesis rates have been corrected for a 300-g standard animal using the correction described in the text. The regression lines are drawn from the formulations described in the text.

synthesis accounts for 42% of the maximum oxygen consumption.

It is clear from the present analysis that protein synthesis can account for a considerable proportion of the metabolic rate, particularly in growing fish; previous estimates of the energetic cost of protein synthesis as a percentage of energetic expenditure for mammals have yielded values of 15–22% (Garlick et al. 1976; Nicholas et al. 1977; Reeds and Lobley 1980). The calculations reported here also suggest that the postprandial increases in oxygen consumption may be principally due to the stimulation in protein synthesis following a meal (for recent reviews on the stimulation of oxygen consumption following feeding, see Jobling (1985) and Soofiani and Hawkins (1985)).

Unfortunately, there is no way of estimating the energetics of protein degradation at present, but clearly this would have to be incorporated in the estimate of the total cost of protein deposition, as the latter is the product of both synthesis and degradation.

This analysis of protein synthesis and degradation rates in whole cod raises two questions for which no quantitative data are unavailable: why are growing fish degrading such a high proportion of the proteins they are synthesising and why are starving fish synthesising so much protein? These questions are brought into sharper focus when we consider the energetic costs of protein synthesis reported above.

Tissue Protein Synthesis and Degradation

The ranking of the tissues in terms of fractional rates of protein synthesis agrees fairly closely with those previously published. Generally the gills and the liver are sites of high levels of synthesis in feeding fish (Haschemeyer and Smith 1979; Smith 1981; Haschemeyer 1983; Pocrnjic et al. 1983; Fauconneau 1985; Houlihan et al. 1986). Although possible reasons for the variations in fractional rate of protein synthesis between these tissues have been discussed by these authors, little supporting evidence has been presented. Our results, showing a reduction in protein synthesis rates in all tissue to a constant level during starvation, are in contrast with some previous studies where particularly the liver and gill have been found to be little affected by starvation (Smith and Haschemeyer 1980; Smith 1981; Haschemeyer 1983; Pocrnjic et al. 1983; Loughna and Goldspink 1984). However, most authors agree that the fractional rate of protein synthesis in the white muscle falls in fasted fish (Jackim and LaRoche 1973; Bouche and Vellas 1975; Smith and Haschemeyer 1980; Haschemeyer 1983; Pocrnjic et al. 1983; Fauconneau 1985) although this is the first account which shows that fish protein synthesis rates in vivo are directly correlated with feeding level.

A comparison between the maximum and minimum rates of protein synthesis shows that there are differences between the tissues in the extent to which their fractional rates of protein synthesis fall with starvation (Table 5). Following a 2-d fast, mammals also show tissue specific differences in the degree to which synthesis is reduced, e.g. gut mucosa, 25% fall; gut serosa, 40%; heart, 39%; skeletal muscle, 66% (McNurlan et al. 1982; Preedy et al. 1983; Garlick 1986). Skeletal muscle is by far the most sensitive to variations in food supply, supporting the belief that this tissue is a major site of protein storage in both mammals and fish.

Of all the tissues the white muscle deserves special discussion. It is the major tissue in terms of weight and protein content and, despite having the lowest fractional rate of protein synthesis, contributes 30% to the total protein synthesis of the whole fish and 40% of the growth. Fauconneau and Arnal (1985) have reported broadly similar results for rainbow trout. It is the tissue which is most responsive to increased ration in terms of the expansibility of its fractional synthesis rates (Table 5). It is the most efficient tissue in terms of the retention of synthesised protein as growth (Fig. 6). White muscle fractional synthesis rates show the clearest relationship to growth, thus indicating that it is the most sensitive tissue to growth changes. In view of these qualities, it is, perhaps, useful to think of white muscle as having, apart from its function in swimming, a role as a protein store, providing raw materials for the high turnover requirements of regulatory tissues during periods of nutritional stress and for the provision of resources for reproductive tissues at appropriate times. White muscle contributed 66% of the protein loss of the whole body during starvation. Furthermore, it is the only tissue in starving fish in which net protein loss exceeds synthesis; this is, perhaps, a further indication that white muscle is the amino acid and energy store for other tissues.

The widely different fractional rates of protein synthesis in the tissues and the wide differences in responsiveness to increased ration raise the question of how isometric growth is brought about (Houlihan et al. 1986). The results presented here clearly show that it is by the linkage of degradation rates to synthesis rates in growing animals that the difference between the two (i.e. the fractional growth rate) is maintained at a constant level in each of the tissues: the tissue-specific level of ration-induced stimulation of protein synthesis. The tissues are like different instruments in an orchestra, some playing piano, some forte; all, however, play at the same rhythm (the growth rate).

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Using the Bootstrap to Assess Statistical Significance in the Cluster Analysis of Species Abundance Data

A. F. L. Nemec[1] and R. O. Brinkhurst

Ocean Ecology Division, Institute of Ocean Sciences, 9860 West Saanich Road, P.O. Box 6000, Sidney, B.C. V8L 4B2

Nemec, A. F. L., and R. O. Brinkhurst. 1988. Using the bootstrap to assess statistical significance in the cluster analysis of species abundance data. Can. J. Fish. Aquat. Sci. 45: 965–970.

Clustering techniques are frequently used to analyze species abundance data, despite a lack of objective criteria for assessing the results of such analyses. We show that a nonparametric statistical technique known as the "bootstrap" can, in certain circumstances, be used to overcome this deficiency. The bootstrap uses the distributional properties of a "bootstrap sample", i.e. a sample obtained by an appropriate resampling of the data, to make statistical inferences about the underlying population. The method is versatile and can be readily applied to complex hypothesis testing problems, since the statistical properties of a bootstrap sample can always be determined by simulation. To illustrate the application of the bootstrap to the cluster analysis of ecological data, we derive a test for the "statistical significance" of clusters of communities and show that two dendrograms can be compared by bootstrapping the Fowlkes–Mallow statistic.

On a fréquemment recours aux techniques d'analyse de grappes pour examiner les données sur l'abondance des espèces, malgré l'absence de critères objectifs d'évaluation des résultats de telles analyses. Le document montre qu'une technique statistique non paramétrique appelée « bootstrap » peut, dans certaines circonstances, aider à combler cette lacune. La technique utilise les propriétés de distribution d'un « échantillon bootstrap », c'est-à-dire un échantillon obtenu par un rééchantillonnage approprié des données, pour produire des inférences statistiques au sujet de la population globale. La méthode est souple et peut s'appliquer facilement à des problèmes mettant en cause des tests d'hypothèses complexes, car les propriétés statistiques d'un « échantillon bootstrap » peuvent toujours être déterminées par simulation. Pour illustrer l'application de la technique « bootstrap » à l'analyse de grappes appliquée à des données écologiques, nous établissons un test mesurant la « signification statistique » de grappes de communautés, et nous montrons que deux dendrogrammes peuvent être comparés en appliquant la technique « bootstrap » à la statistique de Fowlkes–Mallow.

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Studies of ecological communities often employ a cluster analysis of species abundance data. The advantages of cluster analysis are numerous and include flexibility in handling continuous and discrete data, ease of computation, wide accessibility of computer programs, graphical display of results, and intuitive appeal. However, one of the most serious limitations of a cluster analysis is the lack of objective criteria for distinguishing between those features of a dendrogram that reflect real relationships among the underlying communities, i.e. "statistically significant" features, and those that are simply the result of random effects. This deficiency can be attributed to several problems that arise when standard (parametric) methods are applied to the cluster analysis of species abundance data. Firstly, it can be difficult to formulate the null and alternative hypotheses in terms of a probability model that governs the raw abundances. Secondly, it may not be obvious how to define a test statistic, i.e. a quantitative measure of some attribute of the data (dendrogram), that is useful in assessing the plausibility of the null hypothesis. Finally, even if the first two problems can be solved, the transformation from the abundance data to the dendrogram and the evaluation of the test statistic are usually sufficiently complicated that the computation of a *P* value (e.g. see Devore 1987) can be extremely difficult.

In recent years, a nonparametric technique known as the "bootstrap" (Efron 1979; Diaconis and Efron 1983; Efron and Gong 1983) has been applied to various statistical problems in which classical parametric theory fails to produce tractable solutions. For example, Felsenstein (1985) has used the bootstrap to place confidence limits on estimated phylogenies and Smith et al. (1986) have used the method to construct confidence intervals for the similarity between algal communities. The main advantage of the bootstrap over the usual parametric methods is that statistical inferences are based on the distributional properties of an appropriate "bootstrap sample," i.e. a sample that is generated by resampling the data, and not the distributional properties of a sample drawn from the underlying population. Consequently, the detailed specification of a probability model for the data is unnecessary and no complex calculations are required, since the statistical properties of a bootstrap sample are easy to determine (approximately) by simulation, if they cannot be derived analytically.

The bootstrap, when used in conjunction with clustering methods, is an invaluable tool for the analysis of ecological data. We describe two practical applications of the bootstrap to the cluster analysis of species abundance data. In one application, statistically significant clusters are identified by bootstrapping the similarity levels at which successive pairs of clusters are linked in an agglomerative, hierarchical cluster analysis; and in the other, two dendrograms are compared by bootstrapping the Fowlkes–Mallows statistic. The methods described here can easily be generalized to other types of data and clustering techniques, as well as other hypothesis testing problems.

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[1] Present address: International Statistics and Research Corp., P.O. Box 496, Brentwood Bay, B.C. V0S 1A0.

Methods

Assume that there are N biological communities (or sites) of interest and that replicate samples are drawn from each. Let $X = [x_{ij}]$ denote the data matrix, where x_{ij} is the abundance of the ith species, or taxon, in the jth sample. All the abundances are assumed to be measured in the same units (e.g. counts per unit area, dry weight per unit volume, etc.) and all samples, or columns of X, are assumed to be statistically independent. The data martix X will have M rows, corresponding to the total number of species identified in all the samples, and $R = R_1 + R_2 + \ldots + R_N$ columns, with the first R_1 columns corresponding to the R_1 replicate samples drawn from the first community, the next R_2 columns corresponding to R_2 samples from the second community, and so on. We will assume that the number of samples drawn from each community is at least two, i.e. $R_1 \geqslant 2$, $R_2 \geqslant 2, \ldots, R_N \geqslant 2$.

Although there are many ways of performing a cluster analysis of the species abundance matrix X, we will restrict our attention to agglomerative, hierarchical clustering methods. An agglomerative, hierarchical cluster analysis is defined by the specification of a similarity coefficient, which measures the similarity between two communities, and a linkage rule for forming the clusters (for details, see Sneath and Sokal 1973). The results of a cluster analysis are usually displayed as a dendrogram, or tree, with a scale showing the similarity levels at which the clusters are formed (see Fig. 1 and 2). Throughout the paper, the linkages of a dendrogram will be numbered according to decreasing similarity (i.e. the first linkage corresponds to the highest level of similarity and the last $(N-1)$ corresponds to the lowest level of similarity).

Bootstrapping the Abundance Matrix

Bootstrapping the species abundance matrix is a simple way of determining the degree to which random variability within a community (i.e. the variability that is seen among replicate samples) affects the morphology of the dendrogram. Since any statistical inference that is based on the outcome of a cluster analysis must account for this sampling variability, the general method outlined below has many potential applications.

In the present context, the bootstrap can be described as follows. Given an $M \times R$ species abundance matrix X, a bootstrap data matrix X' is formed by randomly sampling, with replacement, R columns from the R columns of X. The columns must be selected in accord with any assumptions that apply to the columns of X. For example, if all of the N communities are assumed to be different, the first R_1 columns of X' must be selected from only the first R_1 columns of X, the next R_2 columns must be selected from the next R_2 columns of X, and so on. In this case, only those columns of X that correspond to replicate samples are interchangeable. On the other hand, if all N communities are assumed to be alike, than all R columns are interchangeable and the columns of X' can be selected from the columns of X without regard to community. If all possible bootstrap matrices were generated, the variability seen in the results of the corresponding cluster analyses should provide a good indication of the sampling variability associated with the cluster analysis of the original data matrix X. In practice, a much smaller number of simulations (NBOOT) is sufficient to establish, with reasonable accuracy, the distributional properties of the bootstrap matrix. These properties can be used to derive tests of statistical significance, as illustrated by the two applications described below.

TABLE 1. Artificial species abundance matrix.

	Station									
	A		B		C		D		E	
Species	5	10	0	0	5	15	0	5	0	0
	15	20	5	0	5	10	45	30	20	10
	0	10	10	15	10	5	5	0	0	0
	5	15	20	15	50	45	20	25	30	40
	20	30	20	30	35	30	15	10	5	10

Significance of Clusters

Cluster analysis is often used to identify "homogeneous groups" or "clusters" of communities. Since a cluster analysis will always group the communities in some fashion, an objective criterion must be applied to distinguish between clusters that reflect "true" differences in the underlying communities, i.e. clusters that are "statistically significant," and clusters that are "artificial," or "random," i.e. those that reflect only the random variability within a community. Real clusters are expected to remain relatively invariant from one set of samples to the next, while artificial clusters are expected to vary with each drawing of the samples. Furthermore, the similarity levels at which random clusters link are expected to exceed the levels at which true clusters are defined, i.e. the random variability within true clusters is less than the variability between true clusters.

Various tests for the statistical significance of clusters, which do not use the bootstrap, have been proposed (e.g. Harper 1978; Strauss 1982; Bock 1985). Although we have made no attempt to carry out an exhaustive review of the literature, the need for a test that can be applied under very general conditions is apparent. Therefore, the development of bootstrap tests seems inevitable. In fact, Verner et al. (1985) used a bootstrap approach to demonstrate the degree to which clusters can differ as a result of the random variability within communities, but did not develop a test for the statistical significance of the clusters. In this section, one such test is described.

Consider the problem of testing whether or not each successive linkage in an agglomerative, hierarchical cluster analysis should be accepted. The null hypothesis of interest is the hypothesis that the two clusters that are linked are sufficiently alike that they can be considered to represent a single community. Under the alternative hypothesis the two clusters represent distinctly different communities and should be retained as separate entities, i.e. the linkage should be rejected. Once a linkage has been rejected, the linkages (at lower levels of similarity) that depend on the rejected linkage are no longer defined and therefore, they do not need to be tested. For example, we

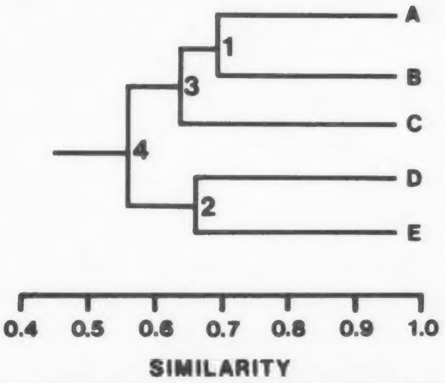

FIG. 1. Dendrogram derived from the (UPGMA, Bray–Curtis) cluster analysis of the artificial species abundance matrix (Table 1). The linkages are numbered in order of decreasing similarity.

cannot test the third and fourth linkages in Fig. 1, if the first linkage is rejected. However, we can test the second linkage.

Each linkage level in a dendrogram is a measure of the similarity between two clusters. To assess whether or not a particular linkage should be accepted, this similarity between clusters must be compared with the similarity that is expected within the cluster defined by the null hypothesis. One way to do this is to restrict attention to those columns of the data matrix that correspond to sites contained in the two clusters under consideration. If this submatrix is bootstrapped under the assumptions of the null hypothesis, and the cluster analysis is applied to each bootstrapped submatrix, the final linkage level is a measure of the similarity within the combined cluster and should be comparable to the linkage level in question, if the null hypothesis is true. If only a small proportion of the bootstrapped values (not more than 5% say, for a 5% level of significance) correspond to a similarity level that is less than or equal to the observed linkage level, then the similarity between the two clusters should be judged to be small enough to reject the null hypothesis.

To illustrate the procedure, consider an artificial example in which two samples are collected at each of five stations (labelled A, B, C, D, E). Assume that a total of five species is identified in the 10 samples and that the species abundance matrix is as shown in Table 1. An UPGMA (unweighted pair group method using arithmetic averages, Sneath and Sokal 1973) cluster analysis of this data matrix, using the Bray–Curtis similarity coefficient (Bray and Curtis 1957) applied to the average (over replicate samples) abundances, yields the dendrogram shown in Fig. 1. To test the statistical significance of the first linkage, the submatrix $X(A,B)$ comprising samples drawn from stations A and B (the two clusters that are linked first) is formed, i.e. $X(A,B)$ is the first four columns of Table 1. Under the null hypothesis that the two stations have identical community structure, the four columns of $X(A,B)$ correspond to replicate samples from a common community. Let $X(A,B)'$ be a bootstrap submatrix that is generated by selecting, with replacement and without regard to station, four columns from the columns of $X(A,B)$, i.e. such that on each draw, each column of $X(A,B)$ has probability 0.25 of being selected. There are 256 different bootstrap submatrices that can be generated. One example is shown below:

$$X(A,B)' = \begin{pmatrix} 0 & 5 & 10 & 0 \\ 0 & 15 & 20 & 0 \\ 15 & 0 & 10 & 15 \\ 15 & 5 & 15 & 15 \\ 30 & 20 & 30 & 30 \end{pmatrix} .$$

Assume that the same clustering procedure that was applied to X is applied to the bootstrap submatrix, i.e. the first two columns and last two columns of $X(A,B)'$ are averaged and an UPGMA cluster analysis, using the Bray–Curtis coefficient, is applied to the average abundances. If the null hypothesis is true, the final linkage level in this cluster analysis of $X(A,B)'$ should be approximately equal to 0.7, the level of similarity at which stations A and B link in the original dendrogram. On the other hand, if the null hypothesis is not true, any differences between the two clusters (stations) will tend to be averaged out by the bootstrapping process and the similarity between the pairs of bootstrapped clusters will tend to exceed the 0.7 similarity level. Let P be the proportion of bootstrapped linkages that are less than or equal to 0.7 when the process is repeated a large number of times (NBOOT). A value of P less than or equal to 5% would suggest that the similarity between the two stations is less than that which could reasonably be expected if the species abundance distributions were the same at the two stations, in which case the null hypothesis should be rejected at the 5% level of significance.

Each of the four linkages in the dendrogram (Fig. 1) can be tested successively, in the same fashion (as long as the corresponding lower order linkages are not rejected). The second linkage is tested by forming the submatrix consisting of columns 7 through 10, the third linkage is tested by forming the submatrix consisting of columns 1 through 6, and the final linkage is tested by bootstrapping the entire data matrix X. Since multiple tests are performed (up to $N-1$), the overall significance level will, in general, be less than the significance level of an individual test. If there is a large number of stations being clustered and a 5% significance level is applied to each linkage, then there is a real possibility that, even when the null hypothesis is true, some of the tests (approximately 5% of the tests) will produce a P value that is less than 5%. One way of dealing with this "multiple comparisons" problem is to use the Bonferroni method, which adjusts the significance level of the individual tests by dividing by the total number of tests or linkages (see Miller 1981).

Comparison of Two Dendrograms

In a second application of the bootstrap, the method is used to compare two dendrograms. Suppose that two data matrices X and Y are subjected to the same cluster analysis and that the resulting dendrograms are to be compared. The problem often arises in environmental monitoring programs when the same sites are sampled on two separate occasions and a cluster analysis is carried out for each set of samples, the results of which are then compared to detect any changes that have occurred in the relationships between the communities. It will be assumed that both data matrices X and Y have the structure described above, i.e. the columns are partitioned according to station, and that the same stations are represented, in the same order, in both. The number of samples taken from each site need not be the same, i.e. the number of columns corresponding to any given station may be different in X and Y. However, both matrices must have the same number of rows (taxa) and each row must correspond to the same taxon. If a taxon is absent in one of the data matrices, a row of zeroes must be entered to ensure the comparability of X and Y, even if it has no effect on the dendrogram. The reason for this will become apparent when the bootstrap calculation is described.

Several statistics that measure the similarity between two dendrograms have been suggested. In this paper the statistic defined by Fowlkes and Mallows (1983) is used as the basis of the bootstrap test, although any other reasonable statistic could have been used just as easily. Fowlkes and Mallows reviewed some of the other measures of the similarity between two dendrograms and discussed the advantages of their statistic.

To define the Fowlkes–Mallows statistic, assume that the two trees being compared are arbitrarily labelled T_1 and T_2. Let T_1 be cut at a level of similarity that produces k clusters and let T_2 be cut at a level that produces l clusters. Following the notation of Fowlkes and Mallows, let m_{ij} be the number of stations that are common to the ith cluster of T_1 and the jth cluster of T_2. The numbering of the clusters is irrelevant. For a given k and l, the Fowlkes–Mallows statistic $B(k,l)$, is defined as

$$B(k,l) = \frac{\sum_{i}\sum_{j} m_{ij}^2 - N}{[(\sum_{i} m_{i\cdot}^2 - N)(\sum_{j} m_{\cdot j}^2 - N)]^{1/2}}$$

where the dot notation indicates summation over a subscript. The marginal totals $m_{i\cdot}$ and $m_{\cdot j}$ are the sizes of the respective clusters.

The Fowlkes–Mallows statistic compares the composition of the clusters defined by the two dendrograms. Its value depends on the "topologies" of the two trees being compared and on the station labels, but it does not depend explicitly on the similarity scale. The minimum value of $B(k,l)$ is zero, which corresponds to no similarity between T_1 and T_2 (at the levels specified by k and l), and the maximum is 1, which occurs when both sets of clusters are identical.

Fowlkes and Mallows (1983) derived the properties of $B(k,l)$ under the null hypothesis that there is a random allocation of the objects (stations) to the clusters, or that T_1 and T_2 are unrelated to each other. Frequently, the null hypothesis of interest is not that two dendrograms bear no resemblance, apart from that which is expected when the two clusterings are random, but that the two clusterings resemble one another because they reflect a common underlying structure in the data. This is often true in the monitoring example described previously where, unless there is strong evidence to the contrary, it is reasonable to assume that the clustering of the stations remains constant over time, since the underlying communities have a stable structure. Since no analytic test of this hypothesis is available, we derive a bootstrap method that is applicable when the rows of the two data matrices correspond to the same measurements (abundances of the same taxa) and replicate samples are available.[2]

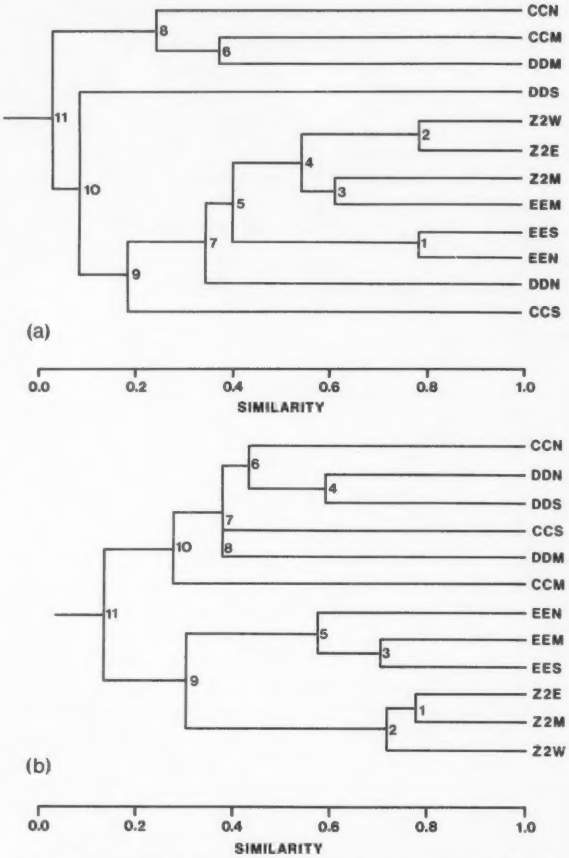

FIG. 2. Dendrograms derived from the (UPGMA, Bray–Curtis) cluster analysis of the Alice Arm/Hastings Arm data for (a) 1982 and (b) 1983. The linkages are numbered in order of decreasing similarity.

The null hypothesis to be tested is that the community structure at any given station is the same for the two data matrices X and Y, i.e. all the samples (X and Y combined) that are drawn from a site are replicate samples from a common community and, therefore, have the same probability distribution. Assuming that this is true for all sites, X and Y are replicate data matrices. If the null hypothesis is true, the cluster analyses of X and Y should produce similar dendrograms and $B(k,l)$ should be relatively large, provided k and l are chosen so that the corresponding clusters are significant and are not the result of random variability within a community. Agreement is not expected among "artificial" clusters, even if the null hypothesis is true.

A bootstrap calculation can be used to help determine whether or not the observed value of $B(k,l)$ is consistent with the null hypothesis, or is unexpectedly small. The Fowlkes–Mallows statistic is bootstrapped by generating NBOOT pairs of bootstrap matrices (X',Y'). The X' matrix of each pair has the same structure as X, i.e. the same number of columns for each station, where each column of X' is a random selection from the combined columns of X and Y that correspond to the appropriate station. The matrix Y' is generated in similar fashion. If $B(k,l)$ is evaluated for each (X',Y') pair, in the same way that it is evaluated for X and Y, its value should be comparable to the value obtained for (X,Y), provided that the null hypothesis

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[2] A referee has pointed out that the test can also be generalized to the case in which T_2 is a fixed clustering pattern, e.g. one that represents the status quo. In that case, the null hypothesis is that the clusters defined by T_2 are the true, or expected, clusters and any deviation of T_1 from these clusters is assumed to be due entirely to random variability within the true clusters. To test this hypothesis, the Fowlkes–Mallows statistic is bootstrapped under the assumptions of the null hypothesis, i.e. using the T_2 clusters to determine which columns of X are interchangeable, a bootstrap species abundance matrix (X') is generated and subjected to the appropriate cluster analysis, the results of which are compared with T_2 by evaluating the Fowlkes–Mallows statistic.

TABLE 2. P values for the linkages shown in Fig. 2.

	Number of simulations (NBOOT)							
	1982				1983			
Linkage	50	100	200	500	50	100	200	500
1	0.080	0.160	0.200	0.184	0.300	0.330	0.310	0.306
2	0.440	0.630	0.550	0.576	0.040	0.260	0.195	0.178
3	0.100	0.080	0.075	0.104	0.080	0.200	0.125	0.092
4	0.060	0.130	0.200	0.130	0.360	0.350	0.430	0.348
5	0.000	0.010	0.005	0.020	0.080	0.060	0.145	0.082
6	0.380	0.240	0.340	0.340	0.380	0.290	0.350	0.432
7	0.060	0.040	0.030	0.056	0.400	0.300	0.350	0.408
8	0.500	0.430	0.455	0.430	0.560	0.490	0.460	0.494
9	0.060	0.030	0.015	0.030	0.000	0.010	0.015	0.008
10	0.100	0.010	0.045	0.034	0.040	0.140	0.110	0.120
11	0.240	0.300	0.285	0.276	0.040	0.020	0.040	0.048

TABLE 3. Comparison of the dendrograms shown in Fig. 2: P values for the Fowlkes–Mallows statistic.

		Number of simulations (NBOOT)			
k	$B(k,k)$	50	100	200	500
11	0.000	0.960	0.920	0.930	0.908
10	0.408	0.860	0.750	0.775	0.802
9	0.289	0.780	0.660	0.720	0.698
8	0.507	0.820	0.750	0.820	0.812
7	0.586	0.760	0.680	0.790	0.744
6	0.500	0.540	0.390	0.455	0.452
5	0.369	0.080	0.070	0.070	0.082
4	0.357	0.020	0.020	0.015	0.008
3	0.611	0.140	0.180	0.110	0.114
2	0.614	0.000	0.000	0.000	0.000

is true. The plausibility of the null hypothesis can be judged by determining the proportion P of bootstrap pairs (X',Y') that result in a $B(k,l)$ that is equal to, or smaller than, the corresponding value for (X,Y). If P is less than or equal to 5%, the null hypothesis that the two trees are the same, apart from random variability, can be rejected at the 5% level of significance.

Examples

The bootstrap procedures[3] described in the preceding sections were applied to the Alice Arm/Hastings Arm species abundance data reported in Kathman et al. (1983, 1984). The data were gathered as part of a program to monitor the effects of mine tailings disposal on the benthic communities of Alice Arm and consist of two abundance matrices, one for each of two years (1982 and 1983) during which samples were collected. All the abundances were normalized to the number of organisms per square metre. During each year, two replicate samples were collected at each of 12 stations located in Alice Arm and Hastings Arm, British Columbia. A total of 79 taxa were identified in the 1982 samples and 67 taxa in the 1983 samples, but only 35 taxa were common to the two years. After inserting rows of zeroes to balance the matrices, both abundance matrices consisted of 111 rows and 24 columns.

An UPGMA cluster analysis, using the Bray–Curtis coefficient (after averaging the abundances over replicates), was applied to each data matrix. This produced the two dendrograms shown in Fig. 2. The significance of the clusters defined by each dendrogram was assessed by generating NBOOT submatrices for each linkage, as described under Significance of Clusters. The results for NBOOT = 50, 100, 200, and 500 independent bootstrap simulations (Table 2, 1982) suggest that the fifth linkage in the 1982 dendrogram should be rejected and that the cluster comprising stations EEN and EES and the cluster comprising EEM, Z2M, Z2E, and Z2W are significantly different. If the fifth linkage is rejected, it is inappropriate to proceed with the linkages that assume that these two clusters can be merged, i.e. the relationships among stations CCS, DDN, and DDS cannot be tested. However, it is appropriate to test the linkages that define the cluster consisting of the three stations CCN, CCM, and DDM (linkages 6 and 8). Examination of the associated P values suggest that this cluster should be accepted. The results for the 1983 dendrogram are somewhat easier to interpret than the 1982 results. The P values in Table 2 (1983) support the conclusion that there are three significant clusters (the EE stations, the Z2 stations, and the rest of the stations).

It is apparent that in both years the amount of variability within a cluster differs from one cluster to the next and, consequently, the significant clusters are not defined at a common level of similarity in either year. This limits the usefulness of the Fowlkes–Mallows statistic, which compares only those clusters that are defined by a single cut of each dendrogram. Despite this limitation, the two dendrograms shown in Fig. 2 were compared by calculating the Fowlkes–Mallows statistic, $B(k,l)$, for $k = l = 11, 10, \ldots, 2$ clusters. The statistical significance of the $B(k,l)$ values was assessed using the bootstrap procedure described under Comparison of Two Dendrograms, with NBOOT = 50, 100, 200, and 500 for each k. The results are presented in Table 3. The differences between the two dendrograms at the "two-cluster" and "four-cluster" levels appear to be statistically significant. Since both linkage levels correspond to one or more statistically significant clusters, it seems reasonable to conclude that the community structure at at least one station differs significantly from one year to the next. Further discussion of these and additional examples of the two bootstrap tests can be found in Brinkhurst (1987), Brinkhurst et al. (1987), Burd and Brinkhurst (1987), and Burd et al. (1987).

Discussion

Advances in computer technology make it feasible to carry out a large number of bootstrap simulations. Consequently, the bootstrap has become a practical alternative to standard parametric approaches to the statistical analysis of data. This is particularly important in connection with the cluster analysis of species abundance data in which parametric models are often lacking or, if available, lead to intractable computations. The present paper demonstrates that when replicate samples are available, the bootstrap can be used to assess the statistical significance of clusters and to compare two dendrograms. Replicate samples permit the (bootstrap) estimation of the variability within a community. It is this "within" variability that provides the necessary standard of comparison by which the statistical significance of clusters and the differences between two dendrograms can be judged. It should be noted the both tests can still be applied when some, or all, of the R_i are equal to 1. Although there has been no attempt to investigate the effect of varying the number of replicates, it is intuitively obvious that the power of the tests decreases when the number of replicates decreases. In fact, when $R_i = 1$ for all i, the test for significant clusters has no power for testing linkages between individual communities.

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[3] FORTRAN programs for carrying out the bootstrap calculations are available upon request.

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The Fowlkes–Mallows Statistic and the Comparison of Two Independently Determined Dendrograms

A. F. L. Nemec[1] and R. O. Brinkhurst

Ocean Ecology Division, Institute of Ocean Sciences, 9860 West Saanich Road, P.O. Box 6000, Sidney, B.C. V8L 4B2

Nemec, A. F. L., and R. O. Brinkhurst. 1988. The Fowlkes–Mallows statistic and the comparison of two independently determined dendrograms. Can. J. Fish. Aquat. Sci. 45: 971–975.

When interpreting the results of a cluster analysis, it is important to understand why specific clustering patterns arise. Comparison of a "dependent" dendrogram with a second, independently determined "covariate" dendrogram (i.e. one that is based solely on information provided by various explanatory variables) is a simple way of investigating the role played by the covariates. The Fowlkes–Mallows statistic, which is a measure of the degree of similarity between two dendrograms, can be used to test the null hypothesis that two dendrograms are unrelated. We show that the Fowlkes–Mallows test can be usefully employed in the systematic comparison of a dependent dendrogram and covariate dendrogram. Since the test is nonparametric, it is applicable to a wide range of problems. As an illustrative example, a species abundance matrix for several benthic communities is subjected to a standard cluster analysis, and the resultant (dependent) dendrogram is compared with a clustering based on the geographic location of the communities. At least some of the clustering seen in the dependent dendrogram can be attributed to the geographic proximity of the stations.

Lorsqu'on interprète les résultats d'une analyse de grappes, il est important de comprendre pourquoi des structures de grappes particulières se présentent. La comparaison d'un dendrogramme « dépendant » avec un deuxième dendrogramme de « covariables » déterminé indépendamment (c.-à-d. fondé uniquement sur l'information fournie par diverses variables explicatives) offre un moyen simple d'étudier le rôle joué par les covariables. La statistique de Fowlkes–Mallows, qui mesure le degré de similitude entre deux dendrogrammes, peut servir à tester l'hypothèse nulle selon laquelle deux dendrogrammes ne présentent pas de corrélation. Nous montrons que le test de Fowlkes–Mallows peut servir efficacement à la comparaison systématique d'un dendrogramme dépendant et d'un dendrogramme de covariables. Puisque le test est non paramétrique, il peut s'appliquer à une vaste gamme de problèmes. À titre d'exemple, une matrice d'abondance des espèces pour plusieurs communautés benthiques est soumise à une analyse de grappes normale, et le dendrogramme (dépendant) qui en résulte est comparé à une structure de grappes fondée sur l'emplacement géographique des communautés. Au moins une partie de l'agrégation observée dans le dendrogramme dépendant peut être attribuée à la proximité géographique des stations.

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Cluster analysis is used to group objects according to similarity. In most applications, a single data set is subjected to an agglomerative, hierarchical cluster analysis and the results are presented as a dendrogram. Central to the interpretation of a dendrogram is the distinction between clusters that are real, i.e. reflect a natural division of the underlying population, and clusters that are spurious. This question is usually resolved by considering the dendrogram, and the data set from which it was derived, in isolation. However, the interpretation of a dendrogram does not end with cluster identification. It is often important to understand why specific clustering patterns arise. This leads to the consideration of factors other than those which were used to construct the dendrogram. The former factors will be referred to as the covariates, or independent variables, while the latter will be referred to as the dependent variables. In the present paper, we focus on the relationship between the covariates and the morphology of the "dependent dendrogram," and not explicitly on the problem of cluster identification.

There are various ways of investigating the role of covariates in a cluster analysis. The approach taken here is the systematic comparison of the dependent dendrogram with a fixed "covariate dendrogram," i.e. a preconceived clustering based on a knowledge of the covariates alone. A comparison of the two dendrograms may lead to the identification of clustering patterns (in the dependent dendrogram) that can be predicted by, or attributed to, clusterings associated with the covariate(s). For example, studies of benthic communities often reveal that clusters derived from an analysis of species abundance data can be explained by environmental factors, such as substrate type, nutrient levels, water temperature, and salinity.

The resemblance between the dependent dendrogram and the covariate dendrogram must be assessed objectively. In particular, it is necessary to determine how much apparent similarity can be expected if there is no relationship between the two dendrograms. Fowlkes and Mallows (1983) defined a measure of the degree of similarity between two dendrograms. The Fowlkes–Mallows statistic is sufficiently simple that its distributional properties are relatively easy to determine, if a certain condition is imposed on the structure of the two dendrograms, and there is a "random allocation" of the objects to the clusters. Consequently, Fowlkes and Mallows were able to derive a nonparametric test of the null hypothesis that two dendrograms are unrelated.

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[1] Present address: International Statistics and Research Corp., P.O. Box 496, Brentwood Bay, B.C. V0S 1A0.

Fowlkes and Mallows illustrated their test by comparing the results of two different types of cluster analysis, which were applied to the same data. In that case, the null hypothesis that the two clusterings are unrelated is unlikely to be true. A more realistic null hypothesis would have specified some kind of relationship between the two dendrograms (see Nemec and Brinkhurst (1988) for a related discussion). Fowlkes and Mallows' inappropriate application of the test lead to the criticism that their null hypothesis is a "straw-man" and lacks relevance in many applications (see the comments (Wallace 1983) that accompany Fowlkes and Mallows 1983). Unfortunately, the criticism belies the usefulness of the Fowlkes–Mallows test when it is applied correctly, e.g. to the comparison of two independently determined dendrograms.

In the present paper, we show that the Fowlkes–Mallows statistic can be usefully employed in the systematic comparison of a dependent dendrogram and a fixed covariate dendrogram. The null distributon is derived by imposing a condition on the structure of the dendrograms that is often more appropriate than the Fowlkes–Mallows condition. An efficient procedure for generating the null distribution and an application of the test are described.

Methods

Let T_1 be the dependent dendrogram, which is derived from an agglomerative, hierarchical cluster analysis of N objects, and let T_2 be a preconceived clustering, which is based on a knowledge of one or more independent variables. It will be assumed that T_1 is subject to random variation, due to variability in the dependent variables, while T_2 is considered fixed.

The Fowlkes–Mallows Statistic

The degree of similarity between T_1 and T_2 can be measured by the statistic defined by Fowlkes and Mallows (1983), which compares the composition of the clusters defined by the two trees. The statistic is evaluated by cutting T_1 at a level of similarity that defines k clusters, i.e. the $(N-k)$th linkage level, if the linkages are numbered in order of decreasing similarity, and by cutting T_2 at a level that defines l clusters. For the given k and l, the Fowlkes–Mallows statistic $B(k,l)$ is defined as:

$$B(k,l) = \frac{\sum_i \sum_j m_{ij}^2 - N}{[(\sum_i m_{i.}^2 - N)(\sum_j m_{.j}^2 - N)]^{1/2}}$$

where m_{ij} is the number of objects that are common to the ith cluster of T_1 and the jth cluster of T_2 ($i = 1,2,\ldots, k; j = 1,2\ldots, l$); the dot notation means summation over the corresponding subscript. The choice of k and l is discussed in the next section.

The Fowlkes–Mallows statistic depends only on the sizes ($m_{i.}$, $i = 1,2,\ldots, k$; $m_{.j}$, $j = 1,2,\ldots l$) and the composition of the clusters, and not on the associated similarity scales. This is an advantage in the present application, since the two scales may not be directly comparable. For example, in a study of benthic communities, T_1 might correspond to a single linkage cluster analysis of species presence–absence data, with the similarity scale defined by the Jaccard coefficient, while T_2 might correspond to a single linkage cluster analysis of water temperatures, with the similarity scale defined by Euclidean distance.

The range of $B(k,l)$ is 0 to 1. The minimum occurs when there is no similarity between the two sets of clusters defined by T_1 and T_2, or when $m_{ij} = 0$ or 1 for all i and j. The latter condition holds in the trivial case of $k = N$ or $l = N$, which implies that the corresponding clusters each contain a single element. More generally, the condition holds when every pair of objects that belongs to the same cluster according to T_1 belongs to two different clusters according to T_2. In cases where $N < kl$, the minimum value of zero cannot be achieved. Wallace (1983) has suggested that $B(k,l)$ should be modified to take this into account. If $k = l$, it is easy to see that $B(k,l) = 1$ when the clusters defined by T_1 and T_2 are identical, i.e. when $m_{ij} = m_{i.} = m_{.j}$ for $i = j$ and $m_{ij} = 0$ for $i \neq j$. In the general case, where $k \neq l$, the maximum is not necessarily 1. These and other properties of $B(k,l)$ are discussed in Fowlkes and Mallows (1983) and Wallace (1983).

Testing the Null Hypothesis

Here the null hypothesis to be tested is that T_1 and T_2 are unrelated, in the sense that the resemblance between T_2 and T_1 is no greater than that which would be expected if T_1 were a random clustering. To test this null hypothesis, the clusters defined at the successive levels of the T_1 hierarchy are compared with the corresponding clusters defined by T_2. This is done by evaluating the Fowlkes–Mallows statistic $B(k,l)$ for $k = l = N-1, N-2,\ldots,2$. Since $B(k,k)$ is expected to be larger when T_1 and T_2 are related than when they are unrelated, the null hypothesis should be rejected when the observed value of $B(k,k)$ is sufficiently large, for at least one k.

One way of determining whether, for a given k and l, the observed value of $B(k,l)$ is large enough to warrant rejection of the null hypothesis is to calculate the associated P value. The P value is the probability that $B(k,l)$ would be at least as large as the observed value if the null hypothesis were true. A small P value (≤ 0.05 for a 5% level of significance) should lead to the rejection of the null hypothesis. To calculate the P value the null distribution of $B(k,l)$ is required.

Null Distribution of the Fowlkes–Mallows Statistic

The null distribution of $B(k,l)$ is computed by assuming that T_1 is generated by random linkages. This means that at any given stage of the cluster analysis, every pair of clusters has an equal probability of being linked at the next stage. When k is large and l is arbitrary, $B(k,l)$ takes on only a small number of values and the derivation of the null distribution is a simple exercise in combinatorics. For example, it is easy to see that for every l:

$$\text{Prob}[B(N,l) = 0] = 1$$

and, if the binomial coefficient $\binom{i}{2}$ is defined to be zero when $i < 2$:

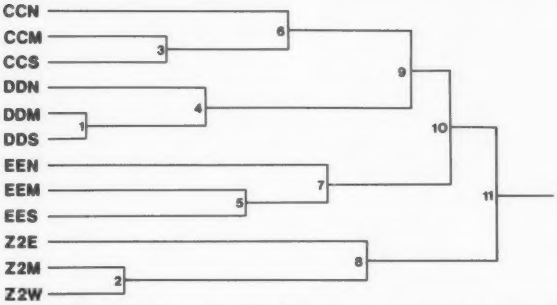

FIG. 1. Geographic tree (T_2). The linkages are numbered in order of increasing distance. The linkage levels are not drawn to scale.

$$\mathrm{Prob}[B(N-1,l) = B_{\max}] = \frac{\binom{m_{\cdot 1}}{2} + \binom{m_{\cdot 2}}{2} + \ldots + \binom{m_{\cdot l}}{2}}{\binom{N}{2}}$$

$$\mathrm{Prob}[B(N-1,l) = 0] = 1 - \mathrm{Prob}[B(N-1,l) = B_{\max}]$$

where

$$B_{\max} = [2/\sum_j (m_{\cdot j}^2 - N)]^{1/2}.$$

As k decreases, the derivation of the null distribution becomes increasingly complex, because $B(k,l)$ takes on more values and the number of different cluster configurations becomes very large. Some idea of the magnitude of the problem can be gained by noting that there are $\binom{N}{2}\binom{N-1}{2}\ldots\binom{k+1}{2}$ different linkage sequences that produce k clusters at the $(N-k)$th linkage level of T_1. The sequences are equally likely under the null hypothesis, but it is obvious that many sequences yield the same cluster configuration. Hence, the values of $B(k,l)$ are by no means unique. Because the correspondence between the linkage sequences and the values of $B(k,l)$ is not easily determined, the exact null distribution of $B(k,l)$ cannot be derived analytically. The distribution could be determined (approximately) by generating every possible linkage sequence (a large random sample of linkage sequences), using a computer, and evaluating $B(k,l)$ for each such sequence. However, this can be quite time consuming if N is large.

One way to make the problem more manageable is to restrict the number of outcomes by imposing some condition on the structure of T_1. Fowlkes and Mallows did this by considering only those trees (T_1 and T_2) with clusters (defined by the specified linkage levels k and l) that are the same size as the clusters of the observed trees, i.e. they considered $m_{i\cdot}$, $i = 1,2,\ldots, k$, and $m_{\cdot j}$, $j = 1,2,\ldots, l$, to be fixed and equal to the observed cluster sizes. We will refer to this condition as "Condition 1." By imposing Condition 1, Fowlkes and Mallows were able to derive analytical expressions for the (conditional) mean and variance of $B(k,k)$. The generalization to $k \neq l$ is straightforward. In the present application, T_2 is assumed to be fixed so there is no loss of generality in constraining the sizes of the T_2 clusters to be $m_{\cdot 1}, m_{\cdot 2},\ldots,m_{\cdot l}$. On the other hand, fixing the sizes of the T_1 clusters is more difficult to justify. Wallace (1983) commented on the drawbacks of imposing Condition 1 and noted that, among other things, it can lead to a loss of information. In the remainder of this section, we discuss a practical alternative to Condition 1.

When $B(k,l)$ is evaluated for $k = l = N-1, N-2,\ldots,2$, it is reasonable to compute the null distribution of $B(k,l)$ by restricting attention to those trees that (at the $(N-k-1)$st linkage level) define the same $k+1$ clusters as the observed T_1. This restriction will be referred to as "Condition 2." Given that Condition 2 holds, it is easy to generate the null distribution of $B(k,l)$ for the specified k and l. When $k = N-1$, the distribution is the same as the unconditional (i.e. no restrictions on the structure of T_1) distribution of $B(k,l)$. Expressions for the unconditional probabilities were given in the first part of this section. Although it has not been possible to generalize the formulas to $k < N-1$, the distribution can easily be determined with the aid of a computer.

Subject to Condition 2, there are $\binom{k+1}{2}$ different cluster configurations that are possible at the $(N-k)$th linkage level, i.e. there are $\binom{k+1}{2}$ different ways of linking two of the $k+1$ clusters that are defined at the $(N-k-1)$st linkage level to form k clusters at the $(N-k)$th level. Every configuration has the same probability under the null hypothesis. For a given k and l, let $\mathbf{M}(k,l) = [m_{ij}(k,l)] = [m_{ij}]$ be the $k \times l$ "matching matrix" where m_{ij} was defined in The Fowlkes–Mallows Statistic. Since the Fowlkes–Mallows statistic $B(k,l)$ depends on T_1 and T_2 only through $\mathbf{M}(k,l)$, the null distribution of $B(k,l)$ can be computed by generating the matching matrices that correspond to the $\binom{k+1}{2}$ different linkages. One can then calculate the associated values of $B(k,l)$ and tabulate their relative frequencies (probabilities).

When the computation is repeated for a sequence of successive linkage levels k and l, i.e. $k = l = N-1, N-2,\ldots,2$, it is useful to note that the ith row of $\mathbf{M}(k,l)$ can be obtained from $\mathbf{M}(k+1,l)$ according to the following recursive formula:

$$m_{ij}(k,l) = m_{i_1 j}(k+1,l) + m_{i_2 j}(k+1,l)$$

if clusters i_1 and i_2 of the $(N-k-1)$st linkage level are linked to form the ith cluster of the $(N-k)$th linkage level. The remaining $k-1$ rows of $\mathbf{M}(k+1,l)$ are unchanged in $\mathbf{M}(k,l)$. A similar relationship holds for the columns $\mathbf{M}(k,l)$ and $\mathbf{M}(k,l+1)$. Given the initial matching matrix $\mathbf{M}(N,N)$, which has ones on the diagonal and zeroes elsewhere, the matching matrices for successive values of k and l can be calculated efficiently by adding the appropriate rows and columns according to the above recursion.

In general, the similarity between T_1 and T_2 that is measured by $B(k+1,l)$ contributes to the similarity that is measured by $B(k,l)$. An advantage of Condition 2 over Condition 1 is that when the clusters defined at the $(N-k-1)$st linkage level are considered fixed, $B(k,l)$ and $B(k+1,l)$ are statistically independent (uncorrelated) for all k (since $B(k+1,l)$ is a constant in that case). In other words, Condition 2 accounts for the contribution to $B(k,l)$ that is due to $B(k+1,l)$. This makes it simple to correct for the fact that the overall significance level of the sequence of tests corresponding to $k = l = N-1, N-2,\ldots 2$ is less than the significance level of an individual test. When the significance levels are evaluated subject to Condition 2, the solution to this "multiple comparisons problem" is to apply an $\alpha_{N-2}(100)\%$ level of significance to each $B(k,k)$ where α_{N-2} satisfies

$$\alpha = 1 - (1 - \alpha_{N-2})^{N-2}$$

and α is the desired overall level of significance (See Miller 1981).

Example

In a program to monitor the effects of mine tailings disposal on the benthic communities of the Alice Arm, samples were

TABLE 1. Comparison of Fig. 1 of this paper and fig. 2b of Nemec and Brinkhurst (1988). Column 1 is the number of clusters k, column 2 gives the Fowlkes–Mallows statistic $B(k,k)$, column 3 gives the corresponding P value when Condition 2 holds, columns 4 and 5 give the mean (μ_2) and standard deviation (σ_2) of $B(k,k)$ when Condition 2 holds, and columns 6 and 7 give the mean (μ_1) and standard deviation (σ_1) of $B(k,k)$ when Condition 1 holds.

(1) k	(2) $B(k,k)$	(3) P	(4) μ_2	(5) σ_2	(6) μ_1	(7) σ_1
11	0.0000	1.0000	0.0152	0.1222	0.0152	0.1222
10	0.4082	0.0364	0.0165	0.0855	0.0371	0.1174
9	0.2887	0.8000	0.2909	0.0653	0.0525	0.1158
8	0.4000	0.1111	0.2112	0.0683	0.0758	0.1146
7	0.4629	0.7143	0.4792	0.0772	0.0982	0.1122
6	0.3536	0.4762	0.3720	0.0792	0.1286	0.1096
5	0.6390	0.0667	0.4794	0.0764	0.1660	0.1053
4	0.7217	0.3000	0.6555	0.0836	0.2099	0.0985
3	0.6983	0.6667	0.7591	0.1292	0.3417	0.0806
2	0.6139	0.6667	0.6100	0.0503	0.5183	0.0451

TABLE 2. Comparison of Fig. 1 of this paper and fig. 2b of Nemec and Brinkhurst (1988). Column 1 is the number of clusters k, column 2 gives the Fowlkes–Mallows statistic $B(k,4)$, column 3 gives the corresponding P value when Condition 2 holds, columns 4 and 5 give the mean (μ_2) and standard deviation (σ_2) of $B(k,4)$ when Condition 2 holds, and columns 6 and 7 give the mean (μ_1) and standard deviation (σ_1) of $B(k,4)$ when Condition 1 holds.

(1) k	(2) $B(k,4)$	(3) P	(4) μ_2	(5) σ_2	(6) μ_1	(7) σ_1
11	0.2887	0.1818	0.0525	0.1113	0.0525	0.1113
10	0.5000	0.0182	0.2368	0.0870	0.0909	0.0996
9	0.5774	0.2000	0.4460	0.0725	0.1050	0.1046
8	0.6455	0.1944	0.5160	0.0775	0.1174	0.1081
7	0.7638	0.0714	0.5729	0.0847	0.1389	0.1070
6	0.6736	0.4762	0.6770	0.0891	0.1575	0.1076
5	0.6667	0.2667	0.6014	0.0812	0.1818	0.1043
4	0.7217	0.2000	0.5916	0.0854	0.2099	0.0985
3	0.5774	0.6667	0.6158	0.0860	0.2624	0.0900
2	0.6325	1.0000	0.8504	0.2673	0.2875	0.2673

collected from several sites in the Alice Arm and Hastings Arm regions of British Columbia over a period of 5 yr (Kathman et al. 1983, 1984; Brinkhurst et al. 1987). The data for 12 different stations that were sampled in 1983 are considered here. The data comprise two samples collected at each of nine stations in the Alice Arm and three control stations in the Hastings Arm. The stations lie along four transects. The three Alice Arm transects are denoted CC, DD, and EE; the Hastings Arm transect is denoted Z2. Each transect has three stations which are distinguished by E or W for east or west, N or S for north or south, or M for the middle station. Abundances were recorded for the 67 taxa that were identified in the 24 samples, and a taxa by community (station) abundance matrix was constructed by averaging the abundances over the two samples taken from each station. A cluster analysis, using the Bray–Curtis similarity coefficient (Bray and Curtis 1957) and the "unweighted pair group method using averages" (UPGMA) (Sneath and Sokal 1973), was applied to the abundance matrix as a means of investigating relationships among the 12 benthic communities (for details, see Kathman et al. 1984; Brinkhurst et al. 1987). The results are summarized in fig. 2b of Nemec and Brinkhurst (1988).

One question that is of interest is whether the observed similarities in the structure of the communities (as measured by the Bray–Curtis coefficient) can be attributed to the geographic proximity of the stations. To test the null hypothesis that the clustering based on the species abundance data is unrelated to the geographic proximity of the stations, a "geographic reference tree" (T_2) was constructed. The geographic tree (Fig. 1) is an UPGMA clustering of the 12 stations, using the geographic distance between the stations as the distance measure. A map showing the location of the stations can be found in Kathman et al. (1984). The four distinct geographic clusters, which correspond to the four transects (CC, DD, EE, and Z2), are readily identified in Fig. 1, at the eighth linkage level.

The two trees T_1 and T_2 were compared by computing the Fowlkes–Mallows statistic, $B(k,l)$, for $k = l = 11, 10, \ldots, 2$. Subject to Condition 2, the null distribution of $B(k,k)$ was generated for each k and was used to compute the associated P value. The distribution was also used to compute the conditional mean and standard deviation of $B(k,k)$. For comparison, the conditional (i.e. subject to Condition 1) mean and standard deviation were computed according to the formulas given by Fowlkes and Mallows.[2] To test whether or not the four geographic clusters (the CC, DD, EE, and Z2 transects) are recovered at any level of T_1, the calculations were repeated with $l = 4$ and $k = 11, 10, \ldots, 2$. The results of the calculations are summarized in Tables 1 and 2.

Examination of the P values in Table 1 suggests that it is unlikely that a random clustering of the stations would have produced the two geographic clusters, i.e. the EE cluster and the Z2 cluster, that are apparent in T_1. It is not surprising to find that the EE stations, which lie on the Alice Arm transect that is farthest from the source of effluent, and the Z2 stations in the Hastings Arm, which are even more remote, follow a geographic clustering pattern. In the absence of other forces, such as pollution, the similarity between benthic communities stations might well be expected to depend on the proximity of the communities. On the other hand, there is no evidence to suggest that the clustering of six remaining stations is geographic.

In this application of the Fowlkes–Mallows test, and in other applications, the failure to reject the null hypothesis (at one or more levels of T_1) does not "prove" that T_1 is a random clustering. It simply means that T_1 exhibits no more similarity to T_2 than that which would be expected if T_1 were generated by a random clustering scheme. The possibility that T_1 is related to some other T_2 is not ruled out. The importance of this distinction was apparent when the 1982 data were analyzed in the same fashion as the 1983 data. In that year, the effect of the mine tailings was quite pronounced. Three stations (CCN, CCM, and DDM) showed a severe depletion in the number and variety of species. The cluster analysis of the abundance matrix identified these three stations as a distinct cluster, despite their quite wide separation (see Nemec and Brinkhurst 1988). Although the cluster would not have been predicted on the basis of the geography of the stations, it is obvious that the clustering of these three stations cannot be considered random if the path of the plume of the mine tailings is taken into consideration. The three stations fell immediately in the path of the plume (as detected in the water column). It is interesting to note that sufficient recovery had taken place by 1983 that the three stations

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[2] A FORTRAN program for calculating the (Condition 2) P value and the conditional (Condition 1 and 2) mean and standard deviation of $B(k,l)$ is available upon request.

CCN, CCM, and DDM were no longer distinguishable from the rest of the CC and DD stations. Further discussion of the Alice Arm data and additional examples of the test described here can be found in Nemec and Brinkhurst (1988), Kathman et al. (1984), Brinkhurst (1987), Brinkhurst et al. (1987), Burd and Brinkhurst (1987), and Burd et al. (1987).

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Empirical Relationships of Phytomacrofaunal Abundance to Plant Biomass and Macrophyte Bed Characteristics[1]

Hélène Cyr[2] and John A. Downing

Département de sciences biologiques, Université de Montréal, C.P. 6128, Succursale "A", Montréal (Québec) H3C 3J7

Cyr, H., and J. A. Downing. 1988. Empirical relationships of phytomacrofaunal abundance to plant biomass and macrophyte bed characteristics. Can. J. Fish. Aquat. Sci. 45: 976–984.

The abundance of phytophilous invertebrates was measured in 13 macrophyte beds and was related, using multiple regression analysis, to the biomass of macrophytes among which the invertebrates were collected, the average plant biomass growing per unit lake area, water and organic matter content of the sediments, total phosphorus concentration in the water, rooting depth of the macrophyte bed, and sampling date. Quantitative analyses are presented for chironomids, cladocerans, cyclopoid copepods, gastropods, water mites (Hydracarina), ostracods, and trichopterans. R^2 values for the regression equations ranged from 0.43 to 0.81. The abundance of invertebrates was best related to the biomass of separate plant species, but equations based only on total plant biomass sometimes had equivalent R^2 values. In general, the abundance of phytophilous invertebrates was positively related to areal plant biomass, sediment organic matter, and lake trophic status and negatively related to depth. The abundance of phytophilous invertebrates generally rose throughout the sampling season. The sign of the relationship with sediment water content, however, varied among invertebrate taxa. Macrophyte beds with high areal plant biomass, in lakes with high total phosphorus concentration, support the greatest abundance of potential invertebrate food for fish and waterfowl.

L'abondance des invertébrés phytophiles a été mesurée dans treize lits de macrophytes; grâce à une analyse par régression multiple, l'abondance a été rapprochée de la biomasse des macrophytes où les invertébrés ont été prélevés, de la biomasse moyenne des plantes par unité de surface lacustre, de la teneur en eau et en matières organiques des sédiments, de la concentration en phosphore total dans l'eau, de la profondeur d'enracinement du lit de macrophytes et de la date d'échantillonnage. Des dosages ont été faits dans le cas des chironomidés, des cladocères, des copépodes cyclopidés, des gastropodes, des hydrachnes (*Hydracarina*), des ostracodes et des trichopterans. Les valeurs R^2 obtenues grâce aux équations de régression variaient entre 0,43 et 0,81. Les meilleurs rapports ont été obtenus entre les invertébrés et la biomasse des espèces végétales considérées une à une, mais les équations où il n'était question que de la biomasse végétale totale avaient parfois des valeurs R^2 équivalentes. En général, l'abondance des invertébrés phytophiles était en corrélation positive avec la biomasse végétale du secteur considéré, avec la teneur en matière organique des sédiments et avec le niveau trophique du lac, mais en corrélation négative avec la profondeur. Généralement, on capturait de plus en plus d'invertébrés phytophiles à mesure que la campagne d'échantillonnage progressait. Le fait que le rapport avec la teneur en eau des sédiments était soit positif, soit négatif, dépendait, cependant, des taxons d'invertébrés considérés. Les lits de macrophytes à biomasse élevée dans les lacs à la concentration élevée en phosphore total recèlent la plus grande abondance d'invertébrés qui peuvent servir à l'alimentation du poisson et de la sauvagine.

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The littoral zones of lakes sustain a highly diversified, abundant, and productive invertebrate fauna, especially when vegetated (Gerking 1964; Pieczyński 1977; Lim and Fernando 1978; Gilinsky 1984). The phytophilic invertebrates are very abundant, usually from 2 to 10 times more abundant than littoral benthos (Pieczyński 1973; Soszka 1975; Vincent et al. 1982), and could therefore play an important role in energy transfer in lakes (Miura et al. 1978). Epiphytic invertebrates represent an important source of food for juvenile and adult fish (Mittelbach 1984; Keast 1985) and for waterfowl (Krull 1970). The abundance of insect larvae in macrophyte beds is also related to insect pest problems in lakeshore areas (Stimac and Leong 1977). It would therefore be of theoretical and of practical interest to predict the abundance of invertebrates in macrophyte beds.

Despite their numerical importance, very little is known about the distribution of epiphytic invertebrates, probably because most work has been based on few, often qualitative samples. Many studies are still based on qualitative sampling, done by hand, with dip nets or with buckets (e.g. Gilinsky 1984; Scheffer et al. 1984). More quantitative samplers are available but many of these samplers yield inaccurate estimates of invertebrate abundance (Downing and Cyr 1985; Downing 1986). Most published results are therefore biased. The problem is worsened by the limited sampling on which most studies are based, despite the notoriously high variability in invertebrate abundance found within and among macrophyte beds (Mrachek 1966; Soszka 1975). In most studies, few replicate samples (n) are collected within a macrophyte bed (e.g. Menzie 1980: $n = 2$; Crowder and Cooper 1982: $n = 3$; Dvořak and Best 1982: $n = 1$; Vincent et al. 1982: $n = 2$; Rabe and Gibson 1984: $n = 1$) and few macrophyte beds (h) are sampled (e.g. Mittelbach 1981, 1984: $h = 2$ and 3, respectively; Biggs and Malthus 1982: $h = 3$; Cattaneo 1983: $h = 1$; Keast 1984: $h = 3$; Rooke 1984, 1986a: $s = 1$ in both cases).

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[1] Publication No. 331 of the Groupe d'écologie des eaux douces de l'Université de Montréal.

[2] Present address: Institute of Ecosystem Studies, Box AB, Millbrook, NY 12545, USA.

Most authors agree that the abundance of plant-dwelling invertebrates in a macrophyte bed is related to the abundance of aquatic plant species (Downing 1986), the physical and chemical characteristics of the environment (Vincent et al. 1982), predation (Crowder and Cooper 1982), competition (Paterson and Fernando 1971), or the emergence of insects (Stimac and Leong 1977). Although suggestive, these results are either semiquantitative or are based on data from few sites and lakes, and they have not yielded any model for predicting the abundance of phytophilous invertebrates. We tested the hypotheses that the abundance of invertebrates in different macrophyte beds is related to (1) the biomass of macrophytes and (2) macrophyte bed characteristics, including plant density, sediment quality, lake trophic status, and rooting depth. The abundance of phytophilous invertebrates is usually positively related to plant density (Macan and Kitching 1972; Crowder and Cooper 1982). Dense macrophyte beds could, for example, reduce fish predation (Crowder and Cooper 1982), increase total periphyton biomass by providing more colonizable substrate (Kowalczewski and Pieczyńska 1976), increase silt sedimentation favorable to detritus feeders (Petr 1968), and reduce wave action detrimental to loosely attached epiphytic invertebrates (Dejoux and Saint-Jean 1972). Sediment quality has also been suggested to influence the distribution of benthic invertebrates (Cole and Weigmann 1983; Vodopich and Cowell 1984). It might therefore be related to the distribution of epiphytic invertebrates which overwinter in the sediments and colonize the plants again in summer (Menzie 1980; Cattaneo 1983). We also expect a positive relationship between the abundance of plant-dwelling invertebrates and the concentration of total phosphorus in the water, suggested by the relationship found between total phosphorus concentration and the biomass of epiphytic and planktonic algae on which epiphytic invertebrates feed (Cattaneo and Kalff 1980; Downing 1981; McQueen et al. 1986).

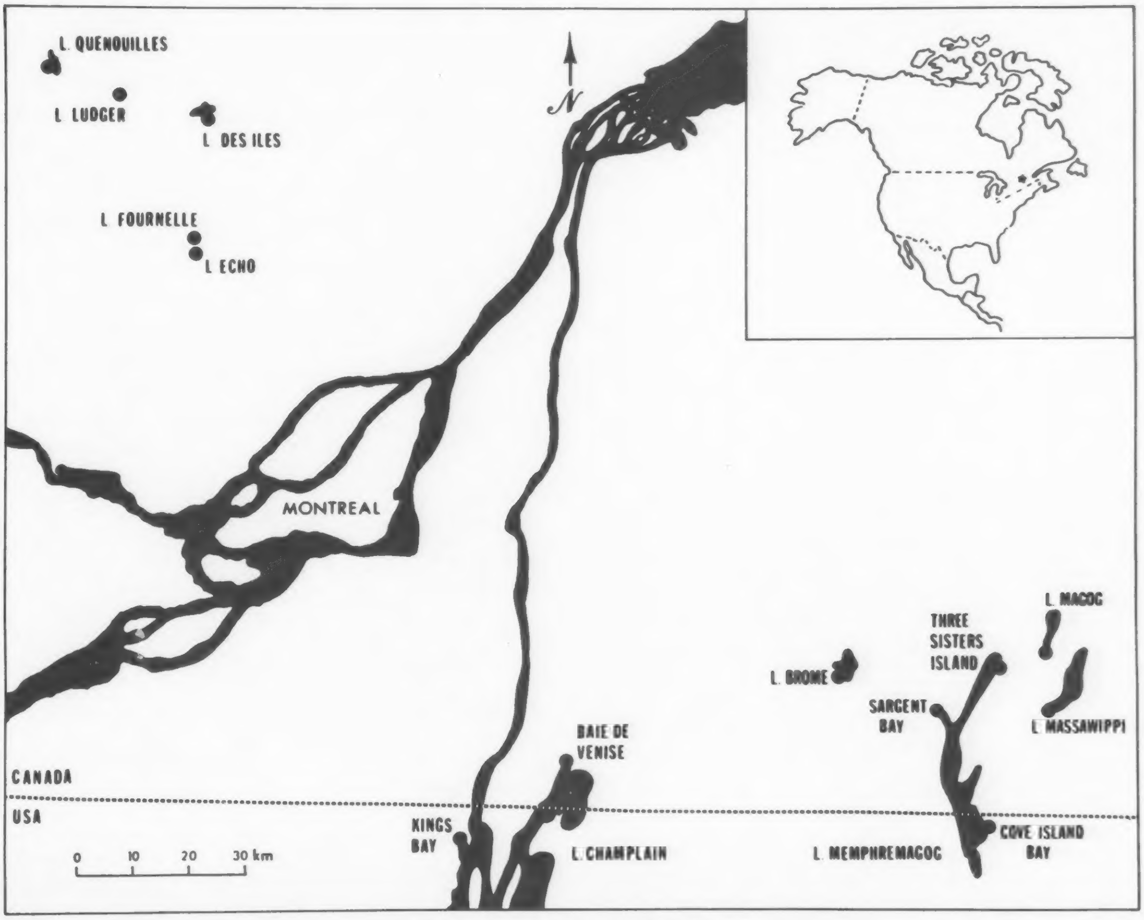

FIG. 1. Location of the sampling sites.

TABLE 1. Characteristics of the 13 sampling sites. The average measures of areal plant biomass (PBA), proportion by weight of sediment water content (SWC) and organic matter content (SOC), total phosphorus concentration in the water around the macrophyte bed (TP), and rooting depth of the macrophyte bed (Z) are presented for each site, with their standard deviations in parentheses. Macrophyte species composition includes all plant species, listed in decreasing order of importance, that represented more than 1% of the total macrophyte biomass: C, *Chara* sp.; CC, *Cabomba caroliniana*; CD, *Ceratophyllum demersum*; EC, *Elodea canadensis*; I, *Isoetes* sp.; J, *Juncus* sp.; M, *Myriophyllum spicatum* and *M. humile* in Lake Des Iles; NF, *Najas flexilis*; NH, *Nitella hyalina*; P, *Potamogeton* sp.; PA, *Potamogeton amplifolius*; PE, a mixture of *Potamogeton epihydrus* and *P. gramineus*; PR, *Potamogeton robbinsii*; S, *Sagittaria* sp.; U, *Utricularia* sp.; VA, *Vallisneria americana*. The sampling day is a numerical date ranging from day 1 (July 3, 1984) to day 55 (August 26, 1984).

Lake	PBA (g/m^2)	SWC	SOC	TP (µg/L)	Z (m)	Macrophyte species composition	Sampling day
Brome	9	—	—	16	1.7	VA, EC	34
(Eagle Island)	(17)			(2)	(0.2)		
Champlain	88	—	—	32	1.8	VA, M, P	42
(Baie de Venise)	(88)			(8)	(0.2)		
Champlain	276	0.25	0.014	12	3.1	VA, PR, M,	54
(Kings Bay)	(177)	(0.06)	(0.005)	(2)	(0.1)	PA, EC	
Des Iles	65	0.36	0.021	7	2.2	M, PR,	55
	(88)	(0.02)	(0.003)	(2)	(0.2)	I, S	
Echo	63	0.48	0.013	11	1.4	PA	12
	(120)	(0.03)	(0.003)	(1)	(0.01)		
Fournelle	256	0.96	0.014	8	2.0	PR, PA, EC	7
	(116)	(0.01)	(0.003)	(2)	(0.2)		
Ludger	40	0.48	0.033	12	1.9	PA, J, U,	27
	(84)	(0.02)	(0.004)	(4)	(0.2)	C, NH, PR	
Magog	131	0.28	0.020	38	1.4	PR, EC, M,	40
	(108)	(0.06)	(0.008)	(12)	(0.04)	CD, P	
Massawippi	397	0.40	0.026	28	2.7	M	14
(Ayer's Cliff)	(428)	(0.04)	(0.004)	(7)	(0.2)		
Memphrémagog	85	0.60	0.035	12	2.0	P, M, VA	1
(Sargent's Bay)	(86)	(0.10)	(0.008)	(2)	(0.6)		
Memphrémagog	48	0.32	0.022	7	3.0	M, PR, VA,	48
(Three Sisters Island)	(80)	(0.03)	(0.00003)	(1)	(0.4)	PE, EC	
Memphrémagog	76	0.19	0.007	12	1.4	P, VA, CC,	21
(Cove Island Bay)	(30)	(0.02)	(0.002)	(4)	(0.1)	NH, EC, NF	
Quenouilles	182	0.46	0.027	10	1.6	PR	28
	(108)	(0.02)	(0.004)	(2)	(0.00)		

Methods

Thirteen macrophyte beds of mixed plant species were sampled from 10 lakes within a 150-km radius of Montréal, Québec (45°31′N, 73°36′W), during July and August 1984 (Fig. 1; Table 1). Macrophyte beds larger than 100 m^2 were sought at sites differing in trophic status and depth and were selected to vary in plant density and species composition. The abundance of phytophilous invertebrates was estimated at each site and related, by regression analysis, to the biomass of plants among which they were found, the characteristics of the macrophyte bed, and the sampling date. The sampling date was included as a covariable in the analysis to compensate for seasonal trends in invertebrate abundance.

Phytomacrofauna Samples

At each site, 15–20 samples of plant-dwelling invertebrates were collected by gentle closure of a 6-L plastic box (Downing 1986) over plants. The samples were distributed at random points along either side of a 50-m transect positioned parallel to shore. Each sample was also taken at a randomly chosen height along the plant stems to estimate the average abundance of invertebrates, regardless of their vertical distribution. We included a wide range of macrophyte abundance and macrophyte species composition into the samples to maximize the range of applicability of our regression equations.

The volume of each phytomacrofauna sample was reduced by filtration through a 100-µm Nitex-mesh filter funnel (Likens and Gilbert 1970) and the samples were kept cold during transport to the laboratory. The invertebrates retained on the 100-µm filter were then carefully washed from the macrophytes and preserved in 80% ethanol (with 1% glycerine to prevent desiccation; Cyr 1986). The macrophytes were separated by species (Fassett 1957), dried at 60°C to constant weight, and weighed (±0.1 mg). All invertebrates in 231 samples were counted at 16× magnification and separated into major taxonomic groups. We collected amphipods, cladocerans, copepods, flatworms (Turbellaria), gastropods, insect larvae, isopods, leeches, nematodes, ostracods, tardigrades, and water mites (Hydracarina). Oligochaetes were often found broken in the samples and were therefore not counted. The abundance of oligochaetes varied among sites and their omission underestimates, although not in a systematic fashion, the total counts of invertebrates. The phytomacrofauna samples provided data on the abundance of invertebrates and on the biomass of plants supporting them.

Macrophyte Bed Characteristics

In each macrophyte bed, we measured the biomass of macrophytes per unit lake area, some sediment characteristics, the total phosphorus concentration of the water surrounding the plants, and the depth at the site. At each site, 25 quadrat samples of plants (112 cm^2; Downing and Anderson 1985) were randomly collected along the 50-m transect used for phytomacrofaunal sampling. The macrophytes were separated by species, dried at 60°C to constant weight and weighed (±0.1 mg). A sediment sample was taken by a diver at the center of each harvested quadrat, using a 5.6-cm-diameter handcorer. The overlying water in the core tube was gently poured out and the top 10 cm of sediments isolated for analysis. The sediments were homogenized and the percentage water and organic matter content measured. The sediment water content was calculated as (WW − DW)/WW where WW is sediment wet weight and DW is the weight of sediments dried at 60°C to constant weight. The sediment organic matter content was estimated as the ash-free dry weight and calculated as (DW − AW)/DW where AW is ash weight from sediments burned at 550°C to constant weight. Water samples for total phosphorus analyses were collected 15–30 cm below the lake surface at 10-m intervals along the 50-m transect. Phosphorus analyses were performed by persulfate digestion, followed by the ascorbic acid colorimetric method (American Public Health Association et al. 1985) with readings taken after 45–60 min. Water depth in the macrophyte bed was also measured (±0.1 m) at 10-m intervals along the transect. Average measures of macrophyte biomass per unit lake area (25 samples), sediment water and organic matter content (25 samples), total phosphorus concentration of the water (6 samples), and rooting depth of the macrophyte bed (6 measures) were calculated and macrophyte species composition was noted at each site (Table 1). Sampling dates were entered in the regressions using a day number ranging from day 1 (July 3, 1984) to day 55 (August 26, 1984) (Table 1).

Statistical Analysis

The relationships between the abundance of invertebrates, the biomass of macrophytes, macrophyte bed characteristics, and sampling date were quantified using forward stepwise linear multiple regression analysis. Separate analyses were performed for each of the common taxonomic groups encountered and for the total of all invertebrates.

The variables used in our analyses were transformed to normalize the residuals and equalize their variances. We transformed the abundance of chironomids, cyclopoids, water mites, ostracods, and the total abundance of invertebrates to their fourth root ($(Y)^{0.25}$), the abundance of cladocerans to logarithms ($\log(Y)$), the abundance of *Bosmina longirostris, Camptocercus* sp., *Chydorus sphaericus, Eurycercus lamellatus*, Sididae, gastropods, and trichopterans to $\log(Y + 1)$, the abundance of other chydorid cladocerans to $\log(1/(Y + 1))$, and the biomass of plant species to either fourth root ($(X)^{0.25}$) or to logarithm ($\log(X + 0.0001)$). Arc-sine transformations for percentages (Draper and Smith 1981, p. 239) were attempted on the ratios of water and organic matter in the sediments, but did not improve the fit of the regression or the distribution of the residuals. Data on the five environmental variables and sampling day were left untransformed.

Two series of regressions were performed: (A) including the total biomass of macrophytes collected in the phytomacrofauna samples and (B) including the biomass of each macrophyte species collected in the phytomacrofauna samples. For each invertebrate taxon, we obtained two equations of the form

$$Y_i = b_1X_1 + b_2X_2 + \ldots + b_kX_k + a$$

where Y_i is the transformed abundance of invertebrates from taxon i, X_1 to X_k are transformed macrophyte biomass collected in the phytomacrofauna samples (either total in equations of type A or separated by species in equations of type B), environmental variables and sampling day, b_1 to b_k are fitted coefficients, and a is the stochastic error term. Only variables with regression coefficients significantly different from zero ($P(t) < 0.05$) were retained in the equations. We obtained equations relating the abundance of each invertebrate taxon to the biomass of plants among which they were collected, macrophyte bed characteristics, and sampling date. Significance of the regression coefficients b_1 to b_k was taken as validation of the relationship between the abundance of epiphytic invertebrates, the biomass of macrophytes, and macrophyte bed characteristics.

Results and Discussion

Both hypotheses were upheld. The regression coefficients for macrophyte biomass and macrophyte bed characteristics were often highly significant. The abundance of phytophilous invertebrates was therefore related to biological, physical, and chemical characteristics of the habitat and varied in a consistent way throughout the sampling period. Multivariate relationships were fitted for the total abundance of invertebrates, the total abundance of cladocerans, and the abundance of 12 other invertebrate taxa (Tables 2 and 3). All equations were highly significant ($P(F) < 0.0001$) and explained 43–81% of the variance in transformed invertebrate abundance.

In most cases, transformations permitted valid analyses to be performed. Unfortunately, the equations for the cladocerans *B. longirostris*, *E. lamellatus*, the gastropods, and the trichopterans had heteroscedastic residuals even after transformation of the dependent and independent variables (Cyr 1986). In all cases, the heteroscedasticity of the residuals resulted in an overestimation of both the overall regression F-values and the t-values for each regression coefficient (Gujarati 1978, p. 199). Too many significant F- and t-values were therefore found (type 1 error). Given the high significance of these equations ($P(F) < 0.0001$; Tables 2 and 3) and of their regression coefficients, however, the results are probably robust to such departures from the homoscedasticity assumptions.

We could not fit equations with unbiased, normal, and homoscedastic residuals for invertebrate taxa that were rare or absent in several lakes, namely amphipods, cladocerans such as Daphnidae (including *Ceriodaphnia* sp., *Daphnia* sp., *Simocephalus* sp.), *Ilyocryptus* sp., *Macrothrix* sp., *Ophryoxus* sp., and *Polyphemus* sp., calanoid and harpacticoid copepods, Hirudinea, insects belonging to the orders Coleoptera, Diptera (Ceratopogonidae and Tipulidae), Ephemeroptera, Lepidoptera, Megaloptera, and Odonata, isopods, nematodes, tardigrades, and turbellarians. The abundance of the most common taxa, however, was strongly related to the biomass of macrophytes, environmental characteristics, and sampling day.

TABLE 2. Multivariate equations relating the abundance of phytophilous invertebrates to total plant biomass collected in phytomacrofaunal samples (BPL), macrophyte bed characteristics, and sampling date (SD). All equations are highly significant ($P(F) < 0.0001$). The adjusted R^2, the F-value, and the effective (n) are presented for each equation. Invertebrate taxa: CHIR, chironomids; CLAD, total cladocerans; BOSM, *Bosmina longirostris*; CAMP, *Camptocercus* sp.; CHYD, *Chydorus sphaericus*; ALON, other Chydorinae; EURY, *Eurycercus lamellatus*; SIDA, Sididae; CYCL, cyclopoids; GAST, gastropods; ACAR, water mites (Hydracarina); OSTR, ostracods; TRIC, trichopterans; TOTAL, all invertebrates retained on a 100-μ filter, excluding the oligochaetes. The abbreviations for macrophyte bed characteristics are as in Table 1.

Equation	Adjusted R^2	F	n
$(\mathrm{CHIR})^{0.25} = 3.2\ (\mathrm{BPL})^{0.25} + 0.004\ \mathrm{PBA} + 0.03\ \mathrm{TP} - 1.0\ Z + 0.01\ \mathrm{SD} + 1.5$	0.62	76	231
$\log(\mathrm{CLAD}) = 0.49 \log(\mathrm{BPL}) + 0.002\ \mathrm{PBA} - 0.5\ \mathrm{SWC} + 47\ \mathrm{SOC} - 0.7\ Z + 0.009\ \mathrm{SD} + 2.9$	0.68	68	193
$\log(\mathrm{BOSM}) = -0.21 \log(\mathrm{BPL}) + 0.009\mathrm{PBA} - 1.4\ \mathrm{SWC} + 97\ \mathrm{SOC} - 0.08\ \mathrm{TP} - 1.6\ Z + 0.03\ \mathrm{SD} + 1.8$	0.75	87	199
$\log(\mathrm{CAMP}) = 0.73 \log(\mathrm{BPL}) - 0.002\ \mathrm{PBA} + 0.04\ \mathrm{TP} + 0.6\ Z - 0.01\ \mathrm{SD} + 0.38$	0.43	36	231
$\log(\mathrm{CHYD}) = 0.29\ \mathrm{BPL} + 0.9\ \mathrm{SWC} + 65\ \mathrm{SOC} + 0.03\ \mathrm{TP} - 0.8\ Z + 0.03\ \mathrm{SD} - 0.1$	0.63	56	198
$\log(1/(\mathrm{ALON})) = -0.55 \log(\mathrm{BPL}) - 0.003\ \mathrm{PBA} - 1.7\ \mathrm{SWC} - 38\ \mathrm{SOC} + 0.6\ Z - 0.03\ \mathrm{SD} - 0.1$	0.49	33	197
$\log(\mathrm{EURY}) = 0.20\ \mathrm{BPL} - 1.6\ \mathrm{SWC} + 40\ \mathrm{SOC} + 0.03\ \mathrm{TP} + 0.6\ Z - 0.04\ \mathrm{SD} - 0.2$	0.76	106	199
$\log(\mathrm{SIDA}) = 0.25 \log(\mathrm{BPL}) + 0.001\ \mathrm{PBA} - 2.1\ \mathrm{SWC} - 0.5\ Z - 0.02\ \mathrm{SD} + 3.5$	0.57	54	198
$(\mathrm{CYCL})^{0.25} = 2.1\ (\mathrm{BPL})^{0.25} + 0.001\ \mathrm{PBA} + 50\ \mathrm{SOC} + 0.02\ \mathrm{TP} + 0.3$	0.50	50	199
$\log(\mathrm{GAST}) = 0.46\ \mathrm{BPL} - 0.006\ \mathrm{PBA} - 0.8\ \mathrm{SWC} - 40\ \mathrm{SOC} + 0.03\ \mathrm{TP} + 0.8\ Z - 0.02\ \mathrm{SD} + 1.1$	0.56	38	199
$(\mathrm{ACAR})^{0.25} = 2.7\ (\mathrm{BPL})^{0.25} - 0.01\ \mathrm{TP} - 0.8\ Z + 0.02\ \mathrm{SD} + 1.3$	0.43	44	229
$(\mathrm{OSTR})^{0.25} = 2.3\ (\mathrm{BPL})^{0.25} - 0.004\ \mathrm{PBA} + 0.09\ \mathrm{TP} + 0.8\ Z + 0.02\ \mathrm{SD} - 1.3$	0.56	58	224
$\log(\mathrm{TRIC}) = 0.33\ \mathrm{BPL} - 7\ \mathrm{SOC} + 0.02\ \mathrm{TP} + 0.009\ \mathrm{SD} + 0.1$	0.43	38	197
$(\mathrm{TOTAL})^{0.25} = 4.3\ (\mathrm{BPL})^{0.25} + 0.002\ \mathrm{PBA} + 58\ \mathrm{SOC} + 0.04\ \mathrm{TP} - 0.9\ Z + 0.03\ \mathrm{SD} + 1.3$	0.61	49	186

TABLE 3. Multivariate equations relating the abundance of phytophilous invertebrates to the biomass of plant species, macrophyte bed characteristics, and sampling date (SD). All equations are highly significant ($P(F) < 0.0001$). The adjusted R^2, the F-value, and the effective (n) are presented for each equation. The abbreviations for invertebrate taxa are as in Table 2; plant species and macrophyte bed characteristics are as in Table 1.

Equation	Adjusted R^2	F	n
$(\mathrm{CHIR})^{0.25} = 2.3\ (\mathrm{J})^{0.25} + 1.8\ (\mathrm{PA})^{0.25} + 1.7\ (\mathrm{PR})^{0.25} + 1.7\ (\mathrm{M})^{0.25} + 1.2\ (\mathrm{CD})^{0.25} + 0.7\ (\mathrm{VA})^{0.25} + 0.005\ \mathrm{PBA} + 0.04\ \mathrm{TP} - 1.1\ Z + 0.01\ \mathrm{SD} + 2.9$	0.59	34	231
$\log(\mathrm{CLAD}) = 0.49\ \mathrm{M} + 0.48\ \mathrm{P} + 0.39\ \mathrm{PA} + 0.15\ \mathrm{PR} + 0.002\ \mathrm{PBA} + 41\ \mathrm{SOC} - 0.8\ Z + 0.02\ \mathrm{SD} + 2.3$	0.70	58	193
$\log(\mathrm{BOSM}) = -0.19 \log(\mathrm{CD}) - 0.19 \log(\mathrm{VA}) - 0.08 \log(\mathrm{M}) - 0.06 \log(\mathrm{PR}) + 0.009\ \mathrm{PBA} - 2.0\ \mathrm{SWC} + 89\ \mathrm{SOC} - 0.09\ \mathrm{TP} - 1.4\ Z + 0.03\ \mathrm{SD} + 0.3$	0.79	75	199
$\log(\mathrm{CAMP}) = 0.23 \log(\mathrm{PA}) + 0.16 \log(\mathrm{M}) - 0.14 \log(\mathrm{VA}) + 0.03\ \mathrm{TP} + 0.2\ Z + 1.2$	0.56	59	231
$\log(\mathrm{CHYD}) = 1.3\ \mathrm{CC} + 1.3\ \mathrm{CD} + 0.5\ \mathrm{M} + 0.3\ \mathrm{VA} + 1.5\ \mathrm{SWC} + 60\ \mathrm{SOC} + 0.2\ \mathrm{TP} - 1.0\ Z + 0.04\ \mathrm{SD} + 0.1$	0.66	45	198
$\log(1/(\mathrm{ALON})) = 0.17 \log(\mathrm{VA}) - 0.13 \log(\mathrm{M}) - 0.20 \log(\mathrm{U}) - 0.24 \log(\mathrm{PA}) - 0.005\ \mathrm{PBA} - 1.3\ \mathrm{SWC} - 31\ \mathrm{SOC} + 0.02\ \mathrm{TP} + 0.8\ Z - 0.03\ \mathrm{SD} - 1.8$	0.62	32	197
$\log(\mathrm{EURY}) = 0.54\ \mathrm{M} - 1.1\ \mathrm{SWC} + 30\ \mathrm{SOC} + 0.03\ \mathrm{TP} + 0.4\ Z - 0.03\ \mathrm{SD} + 0.1$	0.81	145	199
$\log(\mathrm{SIDA}) = 0.22 \log(\mathrm{NH}) + 0.08 \log(\mathrm{PA}) - 0.13 \log(\mathrm{U}) - 0.14 \log(\mathrm{PR}) + 0.003\ \mathrm{PBA} - 1.3\ \mathrm{SWC} + 20\ \mathrm{SOC} - 0.02\ \mathrm{TP} - 0.9\ Z + 3.2$	0.60	34	198
$(\mathrm{CYCL})^{0.25} = 1.4\ (\mathrm{M})^{0.25} + 1.3\ (\mathrm{PA})^{0.25} + 0.6\ (\mathrm{PR})^{0.25} + 0.004\ \mathrm{PBA} + 50\ \mathrm{SOC} - 0.5\ Z + 0.009\ \mathrm{SD} + 2.0$	0.51	30	199
$\log(\mathrm{GAST}) = 8.2\ \mathrm{J} + 1.0\ \mathrm{P} + 1.0\ \mathrm{PA} + 0.5\ \mathrm{PR} + 0.3\ \mathrm{VA} + 0.3\ \mathrm{M} - 0.006\ \mathrm{PBA} - 0.9\ \mathrm{SWC} - 37\ \mathrm{SOC} + 0.04\ \mathrm{TP} + 1.0\ Z - 0.02\ \mathrm{SD} + 0.6$	0.63	29	199
$(\mathrm{ACAR})^{0.25} = 2.0\ (\mathrm{PR})^{0.25} + 1.8\ (\mathrm{PA})^{0.25} + 1.0\ (\mathrm{CD})^{0.25} + 0.6\ (\mathrm{VA})^{0.25} + 0.5\ (\mathrm{M})^{0.25} - 0.002\ \mathrm{PBA} + 0.03\ \mathrm{TP} + 1.3$	0.51	34	229
$(\mathrm{OSTR})^{0.25} = 2.5\ (\mathrm{CD})^{0.25} + 2.1\ (\mathrm{VA})^{0.25} + 1.6\ (\mathrm{PR})^{0.25} + 1.6\ (\mathrm{U})^{0.25} + 1.4\ (\mathrm{EC})^{0.25} + 1.2\ (\mathrm{M})^{0.25} + 0.8\ (\mathrm{PA})^{0.25} + 0.8\ (\mathrm{P})^{0.25} - 0.005\ \mathrm{PBA} + 0.1\ \mathrm{TP} + 1.1\ Z - 0.6$	0.70	47	224
$\log(\mathrm{TRIC}) = 16.0\ \mathrm{NH} + 1.1\ \mathrm{CC} + 0.8\ \mathrm{CD} + 0.7\ \mathrm{PA} + 0.4\ \mathrm{PR} + 0.2\ \mathrm{M} + 0.0007\ \mathrm{PBA} + 0.02\ \mathrm{TP} + 0.01\ \mathrm{SD} - 0.3$	0.52	24	197
$(\mathrm{TOTAL})^{0.25} = 3.2\ (\mathrm{M})^{0.25} + 2.5\ (\mathrm{PA})^{0.25} + 2.4\ (\mathrm{U})^{0.25} + 2.0\ (\mathrm{CD})^{0.25} + 1.9\ (\mathrm{PR})^{0.25} + 1.4\ (\mathrm{VA})^{0.25} + 0.006\ \mathrm{PBA} + 52\ \mathrm{SOC} - 1.9\ Z + 0.04\ \mathrm{SD} + 4.5$	0.59	27	186

Macrophyte Biomass in the Phytomacrofaunal Samples

The abundance of phytophilic invertebrates was in general positively related to macrophyte abundance (Table 4), corroborating the suggestions of Gerking (1957) and Krull (1970). The only exception is the cladoceran *B. longirostris* which was negatively related to the biomass of macrophytes (Table 4). *Bosmina longirostris* are found both among macrophytes and in open water (Pennak 1966; Gliwicz and Rybak 1976). Within macrophyte beds, however, we found more *B. longirostris* when fewer plants were collected, suggesting that they were more abundant in the water around the plants than directly on the plants. The abundance of the eurytopic *C. sphaericus* (Pennak 1966; Lim and Fernando 1978), on the other hand, was positively related to the biomass of macrophytes (Table 4). When undisturbed, *C. sphaericus*, like other chydorids, spends most

TABLE 4. Signs of regression coefficients associated to total plant biomass collected in the phytomacrofaunal samples (BPL) in the equations of type A (Table 2) and to the biomass of each plant species in the equations of type B (Table 3). Partial F-values, a measure of the variation in invertebrate abundance explained by each variable, are given in parentheses; ''ns'' indicates that the regression coefficient is not significantly different from zero ($P(t) > 0.05$); symbols for the species of macrophytes are as in Table 1.

Dependent variable	Type A BPL	Type B										
		CC	CD	EC	J	M	NH	P	PA	PR	U	VA
Chironomidae	+ (166)	ns	+ (7)	ns	+ (12)	+ (66)	ns	ns	+ (82)	+ (67)	ns	+ (9)
Cladocera	+ (77)	ns	ns	ns	ns	+ (99)	ns	+ (5)	+ (18)	+ (9)	ns	ns
Bosmina longirostris	– (8)	ns	– (14)	ns	ns	– (10)	ns	ns	ns	– (5)	ns	– (30)
Camptocercus sp.	+ (76)	ns	ns	ns	ns	+ (45)	ns	ns	+ (79)	ns	ns	– (36)
Chydorus sphaericus	+ (26)	+ (4)	+ (9)	ns	ns	+ (41)	ns	ns	ns	ns	ns	+ (7)
Other Chydorinae[a]	+ (39)	ns	ns	ns	ns	+ (15)	ns	ns	+ (68)	ns	+ (6)	– (18)
Eurycercus lamellatus	+ (20)	ns	ns	ns	ns	+ (79)	ns	ns	ns	ns	ns	ns
Sididae	+ (15)	ns	ns	ns	ns	ns	+ (6)	ns	+ (14)	– (38)	– (5)	ns
Cyclopoida	+ (66)	ns	ns	ns	ns	+ (63)	ns	ns	+ (47)	+ (11)	ns	ns
Gastropoda	+ (88)	ns	ns	ns	+ (10)	+ (19)	ns	+ (13)	+ (79)	+ (50)	ns	+ (12)
Hydracarina	+ (145)	ns	+ (8)	ns	ns	+ (14)	ns	ns	+ (113)	+ (157)	ns	+ (11)
Ostracoda	+ (54)	ns	+ (32)	+ (24)	ns	+ (30)	ns	+ (8)	+ (16)	+ (55)	+ (5)	+ (73)
Trichoptera	+ (75)	+ (7)	+ (8)	ns	ns	+ (21)	+ (4)	ns	+ (58)	+ (66)	ns	ns
Total	+ (169)	ns	+ (13)	ns	ns	+ (140)	ns	ns	+ (87)	+ (57)	+ (6)	+ (16)

[a] The signs of regression coefficients in the equation for the transformed abundance of Chydorinae ($\log(1/(Y + 1))$) were inverted to facilitate comparison with other invertebrate taxa.

of its time attached to solid surfaces (Fryer 1968). *Chydorus sphaericus* is perhaps more dependent on submerged plants, at least for support, than is *B. longirostris*. *Eurycercus lamellatus* is a weed-frequenting cladoceran that is commonly found on *Myriophyllum spicatum* (Fryer 1963; Flössner 1964). Its abundance in our samples was also strongly related to the biomass of *Myriophyllum* spp. (Table 4) which alone accounted for 54% of its variance. *Sida crystallina* is usually found attached to broad-leaved plants, especially *Potamogeton* (Smyly 1952; Entz 1947). The abundance of Sididae, composed mostly of *S. crystallina* and of some *Diaphanosoma* sp., was positively related to the biomass of the broad-leaved *Potamogeton amplifolius* but also to the filamentous macroalga *Nitella hyalina* and was negatively related to the biomass of the narrower *Potamogeton robbinsii* and of the delicate *Utricularia* sp. (Table 4). The abundance of other taxa and of total invertebrates was positively related to plant biomass.

Some invertebrate groups seem to colonize various plant species preferentially, while others seem to be equally attracted to any plant substrate. Comparison of the adjusted R^2 values of the equations including total plant biomass (type A) and the biomass of separate plant species (type B) shows that the abundance of gastropods, water mites (Hydracarina), ostracods, and trichopterans was best related (highest R^2) to the biomass of particular plant species. These equations explained between 7 and 13% more variation in invertebrate abundance than the equations including only total plant biomass (Tables 2 and 3). This supports the general belief that epiphytic invertebrates are related differently to plant species (Andrews and Hasler 1943; Soszka 1975; Gerrish and Bristow 1979; Rooke 1986b). On the other hand, the abundance of chironomids, most cladoceran taxa, and cyclopoid copepods was related equally well ($\Delta R^2 < 0.05$) to the biomass of separate plant species and total plant biomass (Tables 2 and 3). Detailed comparisons of the abundance of epiphytic invertebrates among different plant species are presented elsewhere (Cyr 1986).

Environmental Variables

Biological, physical, and chemical characteristics of the macrophyte bed environment also accounted for variability in the abundance of phytomacroinvertebrates, as suggested by many authors (Stimac and Leong 1977; Vincent et al. 1982; Scheffer et al. 1984).

The abundance of most invertebrate taxa was positively related to the average biomass of plants growing per unit lake area (Table 5). Cladocerans were most abundant in macrophyte beds with high areal plant biomass, corroborating the qualita-

TABLE 5. Signs of regression coefficients (+ and −) associated to macrophyte bed characteristics and sampling day (SD) in the equations of type B (Table 3). The symbols and partial F-values (in parentheses) are as in Table 1. "ns" indicates a regression coefficient that is not significantly different from zero ($P > 0.05$); a dash (—) indicates that the variables were not included in the analysis.

Dependent variable	PBA (g/m²)	SWC	SOC	TP (μg/L)	Z (m)	SD
Chironomidae	+ (29)	—	—	+ (17)	− (34)	+ (7)
Cladocera	+ (68)	ns	+ (149)	ns	− (219)	+ (85)
Bosmina longirostris	+ (271)	− (57)	+ (335)	− (218)	− (135)	+ (65)
Camptocercus sp.	ns	—	—	+ (58)	+ (9)	ns
Chydorus sphaericus	ns	+ (39)	+ (141)	+ (27)	− (155)	+ (117)
Other Chydorinae[a]	+ (77)	+ (19)	+ (30)	− (6)	− (38)	+ (92)
Eurycercus lamellatus	ns	− (32)	+ (66)	+ (57)	+ (41)	− (149)
Sididae	+ (70)	− (49)	+ (24)	− (12)	− (165)	ns
Cyclopoida	+ (50)	ns	+ (46)	ns	− (17)	+ (5)
Gastropoda	− (116)	− (14)	− (56)	+ (44)	+ (84)	− (32)
Hydracarina	− (21)	—	—	+ (30)	ns	ns
Ostracoda	− (66)	—	—	+ (151)	+ (49)	ns
Trichoptera	+ (7)	ns	ns	+ (60)	ns	+ (65)
Total	+ (56)	ns	+ (20)	ns	− (110)	+ (56)

[a] The signs of regression coefficients in the equation for the transformed abundance of Chydorinae ($\log(1/(Y + 1))$ were inverted to facilitate comparison with other invertebrate taxa.

tive observations of Smyly (1952). The abundance of Sididae, chironomids, and trichopterans was also positively related to areal plant biomass. These invertebrate taxa are important prey of littoral fish (Gerking 1962; Fairchild 1982), and their large abundance in dense macrophyte beds could therefore result from reduced fish predation (Crowder and Cooper 1982). High areal plant biomass, on the other hand, supported few gastropods (Table 5), contrary to the expectation of Økland (1983).

The abundance of many taxa of plant-dwelling invertebrates was also related to sediment quality (Table 5). Sediment water and organic matter content were strongly related to the abundance of most cladoceran groups ($P < 0.0001$; Table 5), corroborating the qualitative observations of Smyly (1952). Sediment characteristics are indeed likely to influence at least the distribution of chydorid cladocerans which are found both among the vegetation and in the sediments (Fryer 1963, 1968). The abundance of gastropods was negatively related to sediment water content, possibly from the lack of support offered by fluid sediments (Økland 1983). The effect of sediment water content varied among invertebrate taxa, while the organic matter content was mostly positively related to invertebrate abundance.

The abundance of most invertebrate taxa was positively related to total phosphorus levels in the water (Table 5). This is not surprising, since the biomass of epiphytic and planktonic algae, on which the invertebrates feed (Downing 1981; Cattaneo 1983), is also positively related to the total phosphorus concentration in the water column (Cattaneo and Kalff 1980; McQueen et al. 1986). The abundance of *B. longirostris*, Chydorinae (excluding *Camptocercus* sp. and *C. sphaericus*), and Sididae, however, was negatively related to total phosphorus concentrations ($P < 0.05$; Table 5). Young (1945) and Quade (1969) also found *S. crystallina* mostly in clear littoral zones with low periphyton biomass. This is possibly due to the inhibitory effect of high seston concentration on the feeding of *S. crystallina* (Downing 1981). In general, more epiphytic invertebrates were found in eutrophic lakes.

Depth has a significant influence on the abundance of most taxa of plant-dwelling invertebrates. We sampled macrophyte beds growing between depths of 1.4 and 3.1 m. The total abundance of epiphytic invertebrates was negatively related to depth ($P < 0.0001$; Table 5), corroborating the observations of Soszka (1975). Various invertebrate taxa, however, responded differently to depth. The abundance of gastropods was positively related to depth ($P < 0.0001$; Table 5), contrary to the observations of Stańczykowska (1960), who found no difference in gastropod abundance on either of five plant species between shallow and deep (about 5 m) portions of the littoral zone. Chironomids, on the other hand, were negatively related to depth ($P < 0.001$; Table 5), a result which is consistent with the observations of Entz (1947) and Vodopich and Cowell (1984, benthic *Procladius culciformis*) but different from those of Soszka (1975). Cladocerans and cyclopoid copepods were also more abundant in shallow macrophyte beds (Table 5).

Seasonal Effect

We sampled all macrophyte beds in the shortest time possible to minimize seasonal variability in invertebrate abundance among sampling sites. Sampling each macrophyte bed took about 130 person-hours of laboratory and field work (see also Downing and Cyr 1985) and sampling trips were spaced as closely as possible. All phytomacrofauna samples were collected during July and August, excluding the fall period where the largest increase in invertebrate abundance is usually observed (Smock and Stoneburner 1980; Rooke 1986a). Despite these precautions, the abundance of most invertebrate taxa in our samples increased systematically through the summer ($P < 0.05$; Table 5), as suggested by Mrachek (1966), Soszka (1975), Keast (1985), and Rooke (1986a). The introduction of sampling date in the multivariate equations helped explain up to 25% more variance in invertebrate abundance among samples (Cyr 1986, appendix F). Total invertebrate abundance and the abundance of chironomids, cladocerans, cyclopoid copepods, and trichopterans increased through the summer ($P < 0.05$; Table 5). Our results differ from those of Mrachek (1966) who found, within a lake, a decrease in the abundance of chironomids and no variation in trichopteran numbers throughout the season. The abundance of gastropods per unit plant biomass, on the other hand, decreased from July to August ($P < 0.0001$; Table 5). Plant biomass therefore increases faster than the abundance of gastropods, as suggested by Pip and Stewart (1976), but slower than the abundance of most other invertebrate taxa.

Potentially Advantageous Macrophyte Beds for Fish and Waterfowl

Before our equations can be used for the prediction of phytomacrofaunal abundance, they should be validated using independent observations (Berk 1984). Unfortunately, this is impossible, since so few quantitative data have been published on the abundance of epiphytic invertebrates. Our results, however, can be summarized for practical use in fishery and waterfowl management. These results must be used carefully, since the accessibility of invertebrates also influences their availability as food for fish and waterfowl (Crowder and Cooper 1982; Gilinsky 1984). Large cladocerans (*E. lamellatus*, *S. crystallina*), gastropods, and insect larvae are the most important food source for fish (Gerking 1962; Fryer 1963; Fairchild 1983; Mittelbach 1984). Macrophyte beds supporting large abundances of these invertebrates could potentially be the most important for fisheries. Our sampling sites ranged from low plant biomass per unit lake area to biomasses greater than the world average (310 g/m^2; Duarte et al. 1986), had a wide range of sediment water content, generally low organic matter content, and were located in oligomesotrophic to eutrophic waters, depths of 1.4–3.1 m. Macrophyte beds with high plant biomass per unit lake area, covering sediments of low water content in eutrophic lakes, yielded the highest abundances of fish food organisms per unit macrophyte biomass (Table 5). Crowder and Cooper (1982), however, found that the feeding efficiency of fish decreased with increasing plant density and that fish grew best at intermediate plant density. Within the range of our sampling sites, sediment organic matter content and depth did not affect the abundance of fish food invertebrate taxa in any consistent way. Waterfowl feed mostly on amphipods and aquatic insect larvae (Moyle 1961; Danell and Sjöberg 1980). We found no consistent pattern in the distribution of amphipods, which were only rare components of the phytomacrofauna in 10 of our 13 sites. The abundance of chironomid and trichopteran larvae per unit plant biomass, however, was higher in macrophyte beds with high areal plant biomass located in shallow macrophyte beds in waters of high total phosphorus concentration (Table 5).

Because the size of macrophyte beds is the prime determinant of the total abundance of phytophilous invertebrates in lakes (Smirnov 1963; Głowacka et al. 1976), general enhancement of macrophyte abundance could lead to increased fish (Durocher et al. 1984) and waterfowl abundance. This research has shown, however, that macrophyte species composition, macrophyte standing stock, sediment characteristics, total phosphorus concentration in the water around the plants, rooting depth of the macrophyte bed, and sampling date are also strongly related to the total abundance of phytomacroinvertebrates and to the abundance of individual invertebrate taxa. The abundance of invertebrates in the littoral zones of lakes is a multivariate correlate of many characteristics of the littoral habitat.

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Thermal Significance of the Topographical Distribution of Blubber in Ringed Seals (*Phoca hispida*)

Morten Ryg

Division of General Physiology, University of Oslo, Box 1051, Blindern, 0316 Oslo 3, Norway

Thomas G. Smith

Department of Fisheries and Oceans, Arctic Biological Station, Ste-Anne-de-Bellevue, Que. H9X 3R4

and Nils Are Øritsland

Division of General Physiology, University of Oslo, Box 1051, Blindern, 0316 Oslo 3, Norway
and
Norwegian Polar Institute, Box 158, 1330 Oslo Lufthavn, Norway

Ryg, M., T. G., Smith, and N. A. Øritsland. 1988. Thermal significance of the topographical distribution of blubber in ringed seals (*Phoca hispida*). Can. J. Fish. Aquat. Sci. 45: 985–992.

The distribution of blubber in ringed seals (*Phoca hispida*) and relationships between surface area, body mass, and linear dimensions are described. The blubber was distributed in such a way that the ratio of blubber thickness to body radius is nearly constant over the body, maximizing the available blubber for insulation. The hind part of the body has a higher thickness to radius ratio and is thus "overinsulated." During periods of mass loss, fat is lost fastest from this overinsulated region, thus reducing the negative thermal effects of the fat loss. We present formulae for calculating body surface area and an effective, or "equivalent blubber thickness," for calculations of heat loss and suggest that these formulae are independent of size and shape. By combining these equations, we arrive at a general formula for calculating a lower limit for heat loss from marine mammals. According to this formula, thermal stability can be maintained when blubber is lost if mass is simultaneously lost from the body core.

On décrit la distribution de la graisse chez le phoque annelé (*Phoca hispida*) et les relations entre la superficie du corps, la masse corporelle et les dimensions linéaires. La graisse est distribuée de telle façon que le rapport entre l'épaisseur de la graisse et le rayon du corps est presque constant sur toute la longueur du corps, ce qui maximise la quantité de graisse disponible comme isolant. La partie postérieure du corps montre un rapport plus élevé entre l'épaisseur et le rayon et est donc « surisolée ». Pendant les périodes de perte de masse, on observe une perte plus rapide de graisse dans cette région surisolée, ce qui en réduit ainsi les incidences thermiques négatives. Les auteurs présentent des formules pour le calcul de la superficie du corps et un « facteur d'épaisseur équivalente » ou efficace de la graisse pour le calcul de la perte de chaleur et indiquent que ces formules sont indépendantes de la taille et de la forme. En regroupant ces équations, ils obtiennent une formule générale pour calculer la limite inférieure de la perte thermique chez les mammifères marins. Selon cette formule, on peut maintenir la stabilité thermique quand la graisse est perdue, s'il y a perte simultanée de masse dans la partie centrale du corps.

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The blubber layer in aquatic mammals has multiple functions. It is an energy reserve, adjusts buoyancy, streamlines the body, and acts as thermal insulation. It may not be possible to optimize all these functions simultaneously. The conflict between energy storage and thermal insulation has been recognized (Bryden 1968; Stewart and Lavigne 1980). Since thermal, mechanical, or other constraints often lead to peculiar topographical distributions of fat in mammals (Pond 1978), it is conceivable that the blubber of marine mammals has a characteristic topographical distribution which could serve to solve the conflicts between the various functions of the blubber. Here we investigate the topographical distribution of blubber in ringed seals (*Phoca hispida*) and its significance for the insulation/energy storage conflict.

Whereas heat flow through a plane wall is inversely proportional to the wall thickness, the heat loss per unit length of the cylindrical body depends on the ratio between wall thickness and radius. For calculations of heat loss from a real body, one can consider the body as a series of cylindrical elements and calculate the total heat loss as the sum of the heat losses from each element. It might be preferable, in order to use the simpler equation for heat loss through a plane wall (see eq. (5) below), to define an *equivalent thickness* as the thickness of a plane wall that would allow the same heat loss as the physical body in question, given the same conductivities, temperature differences, and surface areas. In this paper, equivalent thicknesses were computed from data on blubber distribution and body dimensions. Its usefulness for calculating heat loss was tested by comparing calculated with measured postmortem cooling rates. Finally, we provide size- and shape-independent equations for calculating surface area, equivalent thickness, and heat loss from body mass, standard body length, and body composition.

Methods

Abbreviations and units used are as follows: BW = total body mass (kilograms), LBW = lean body mass (kilograms), L = standard body length (metres), A = surface area (square metres), H = heat flow (watts), r = radius (metres), d = blubber thickness (metres), T = temperature (degree Celsius), k = conductivity (watts per metre per degree Celsius), and C = specific heat (joules per kilogram per degree Celsius).

Collection of Data

Ninety ringed seals were shot from the beginning of April to late June on two consecutive years (1985 and 1986), 19 from the Barents Sea and 71 from Kongsfjorden (78°55′N, 11°58′E) on Svalbard. The animals were weighed and standard measurements taken (American Society of Mammologists 1967). Girths were measured around the snout and head, at every 10 cm behind the snout, back to just in front of the anus. Surface area of spread and folded fore- and hindflippers was measured by drawing the contours on paper and measuring these paper areas with a planigraph. The measured areas were multiplied by 2 to get total surface area for each flipper. The animals were aged by the annular growth rings in the canine cementum (Smith 1973). Reproductive status of females was determined by inspection of the uteri, nulliparous females being classified as immature. Males were classified as mature if they had the blackened face and scent characteristic of a "tiggak," a rutting ringed seal male (McLaren 1958).

Blubber thicknesses dorsally and ventrally on the head were measured at incisions through the skin and blubber. The sculp (skin with attached blubber) was carefully dissected from the body core, placed on a flat surface, and stretched out so that sculp length was equal to the standard length of the animal. The blubber thickness was measured at every 10 cm across the length and width of the sculp. Sculp width was measured at every 10 cm along the length.

Blubber mass was determined by subtracting skin mass from sculp mass, after thoroughly removing the blubber from the skin. Skin thicknesses at one position on the body (ventrally behind the front flippers) and one on the head (ventrally beneath the eyes) were measured to the nearest 0.1 mm with a precision caliper.

Postmortem cooling rates were measured on three animals in air (0 to −5°C) and five in ice water (−0.2°C) by laying the freshly killed animals in cracks in the sea ice. Temperatures were measured centrally in the abdomen by forcing a thermometer through a narrow hole in the abdominal wall. The hole was made narrow enough to prevent water from entering. Animals were lying on their backs, and the bodies were shielded from sunlight. Partly because of technical difficulties, and partly because the sampling program evolved, the data set is not complete for all animals.

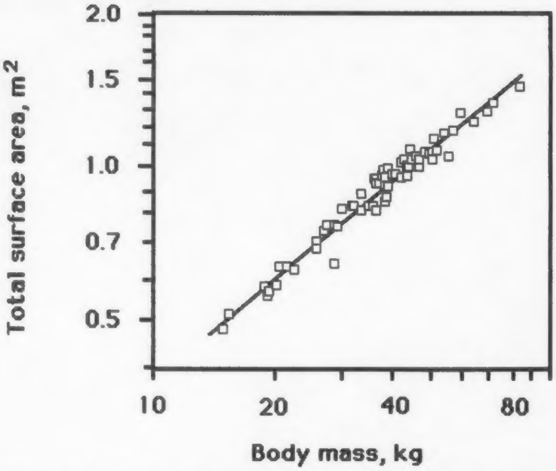

FIG. 1. Relationship between total surface area (with flippers spread) and body mass in ringed seals.

Data Analysis

Surface areas were calculated from the whole-body measurements, by regarding the seal as a series of truncated cones, or by correcting skin area, calculated as a series of trapezia, for shrinkage. The shrinkage factor was calculated from the maximum girth of the whole animal and maximum width of the sculp. Both methods were employed for most seals. With a paired t-test, the two methods did not give significantly different results.

If one considers the body as a series of n cylindrical elements of radius r_i and length L/n, the approximate surface area of the body (including head) is given by

$$(1)\quad A_{\mathrm{body}} = \Sigma 2\pi r_i L/n = 2\pi L r_{\mathrm{mean}}$$

The r_{mean} of a cylinder and a cone is obviously R (maximum radius) and $0.5 \cdot R$, respectively. The r_{mean} for the ellipsoid can be found by rearranging the general formula for an ellipse with axes L and $2R$, to $r = \sqrt{R^2 - (2Rl/L)^2}$, and integrating to find r_{mean}:

$$(2)\quad r_{\mathrm{mean}} = \int_{-L/2}^{L/2} 1/L \cdot \sqrt{R^2 - (2Rl/L)^2}\, dl.$$

Substituting $g = 2l/L$ gives

$$(3)\quad r_{\mathrm{mean}} = R/2 \int_{-1}^{1} \sqrt{(1-g^2)}\, dg = R/4(\arcsin 1 - \arcsin(-1)) = \pi R/4.$$

By expressing R in terms of volume and length of the three geometrical shapes, one finds that the mean radius can be expressed by

$$(4)\quad r_{\mathrm{mean}} = a \cdot \sqrt{\mathrm{Volume/length}}$$

where a is 0.49 for the cone, 0.52 for the ellipsoid, and 0.56 for the cylinder. The differences between these geometrical figures are more extreme than the shape differences between different marine mammals. For work with marine mammals, eq. (4) can probably be regarded as independent of shape and size. If one disregards differences in density and errors intro-

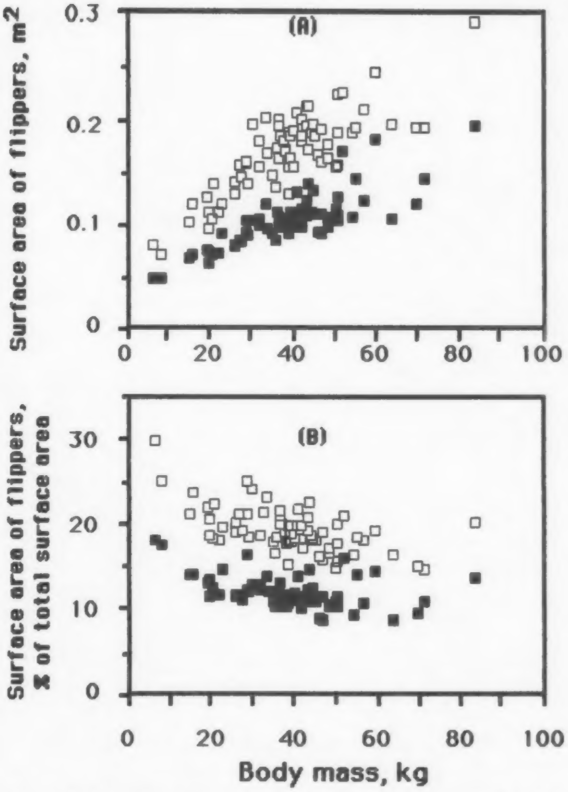

FIG. 2. Relationship between body mass and surface area of spread (□) and folded (■) flippers as (A) square metres and (B) percent of total surface area.

duced by the mass of the appendages, body surface area should thus be proportional to the square root of the product of body mass and body length.

Average blubber thicknesses and blubber thicknesses dorsally, laterally, and ventrally at standard points corresponding to snout, head, and 10, 20, 30, 40, 50, 60, 70, and 80% of standard body length behind the snout were calculated by linear interpolation between the measured values. Body radii at the standard points (see above) were calculated by dividing the interpolated girths by 2π.

Heat transfer across plane and cylindrical walls with thickness d and surface area A is given by

$$(5)\quad H_{\text{plane}} = kA\Delta T/d$$

$$(6)\quad H_{\text{cylinder}} = 2\pi kL\Delta T/\log_e(r/(r-d)) = kA\Delta T/r\cdot\log_e(r/(r-d))$$

where k is the conductivity of the wall material, ΔT is the (constant) temperature difference across the wall, and r and L are the radius and length of the cylinder (Sears 1958). By comparing eq. (5) and (6), the equivalent thickness of a cylindrical body would be $d_{\text{eq}} = r\cdot\log_e(r/r-d)$. On extending this formula to apply to a whole animal, we consider the body as a series of cylindrical elements. Accordingly, the equivalent thickness for an animal was calculated from a formula obtained by equating eq. (5), with d_{eq} in the denominator, with a sum giving the heat losses for a series of cylindrical elements. Surface areas were calculated as the sum of the surface areas of the cylindrical elements on both sides of the equation. Rearranging terms, the expression for the equivalent thickness becomes

$$(7)\quad d_{\text{eq}} = \frac{\sum_{i=1}^{n} r_i\Delta l_i}{\sum_{i=1}^{n} \Delta l_i/\log_e(r_i/(r_i-d_i))}$$

where r_i and d_i are radius and mean blubber thickness at each standard point (see above) and Δl_i is the length of each cylindrical element. Mean blubber thickness for the whole animal was calculated by dividing blubber mass by body surface area and blubber density.

Since data are seldom available for calculating equivalent thickness from eq. (7), we wanted to develop an empirical relationship between equivalent thickness and more commonly obtainable data. Observing that, for each cylindrical element, the surface area is $2\pi rL$ and $r/(r-d) = \sqrt{\text{total volume/core volume}}$, and disregarding differences in density, eq. (6) can be rewritten:

$$(8)\quad H = kA\Delta T/0.5r\log_e(\text{BW/LBW}).$$

Comparing eq. (8) and (5), it seems reasonable to relate the equivalent thickness to the product of mean radius and the natural logarithm of total body mass divided by lean body mass. Mean radius can be replaced by the square root of body mass divided by body length (eq. (4)).

Measured cooling rates of dead animals were compared with cooling rates calculated from the equivalent thickness and surface area of a 10-cm midsection of each animal, assuming a blubber conductivity of $0.2\ \text{W}\cdot\text{m}^{-1}\cdot{}^{\circ}\text{C}^{-1}$ (Scholander et al. 1950). When there is no heat production within the animal, and one assumes that the core temperature in the section is uniform, the core temperature should decrease according to Newton's law of cooling:

$$(9)\quad \log_e(T_{db}-T_a) = \log_e(T_{db,\text{initial}}-T_a) - bt$$

where t is the elapsed time since the cooling started. The logarithmic cooling rate b can be expressed by

$$(10)\quad b = k\cdot A_{\text{body}}/(c\cdot\text{BW}\cdot d)$$

where the thickness d includes skin thickness. The specific heat (c) was calculated as a weighted average (based on body composition at the site of temperature measurement) of specific heats of fat and lean tissues (Minard 1970). The reason why we use only the midsection of the seal to calculate the cooling rate is that as the animal cools, the temperature drops fastest at the ends, and so, the assumption of a uniform core temperature is violated.

Statistics

Least squares regression analyses were done on relationships between surface areas and equivalent thicknesses on expressions derived from body mass, body composition, and linear dimensions. The analysis was based on actually measured variables, and not corrected for blood loss. The data presented in the figures are also based on uncorrected values. To evaluate the applicability of the equations for live animals, the regressions were also calculated after adding skin to blubber thickness in the calculations of equivalent thickness, correcting body mass for an estimated blood loss of 10 or 15% (St. Aubin et al. 1978), and replacing lean body mass with core mass (corrected body mass minus sculp mass). Since body length does not change

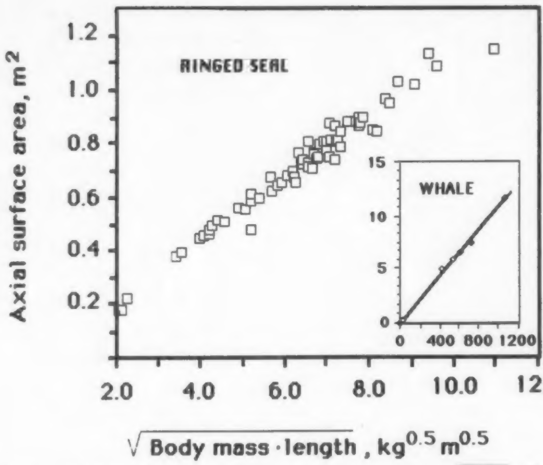

FIG. 3. Relationship between body surface area and $\sqrt{BW\cdot L}$. ☐, *Phoca hispida*; ◆, *Balaenoptera physalus* (Lockyer and Waters 1986); ◇, *Balaenoptera borealis* (Lockyer and Waters 1986).

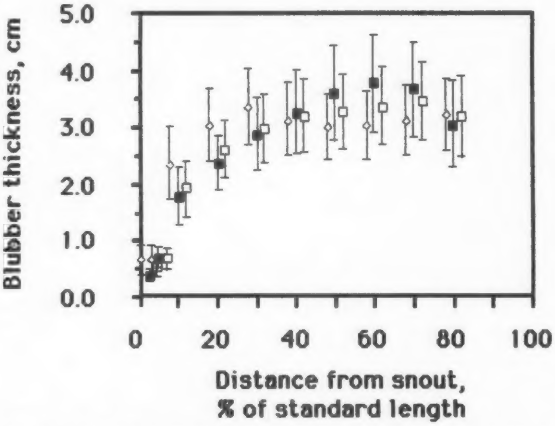

FIG. 4. Blubber thickness dorsally (■), laterally (☐), and ventrally (◇) along the body of seals shot before 15 May.

with bleeding, measured girths were corrected with a factor that was the square root of the correction factor for body mass. Differences between measured and calculated cooling rates were tested using Student's *t*-test for paired data.

Results

Surface Areas

Total surface area (axial and appendicular, with spread flippers) was proportional to the 0.69th power of body mass (Fig. 1). The exponent was not significantly different from 2/3. The regression equation of total surface area on $BW^{2/3}$ was

$$(11)\quad A_{\text{total}} = 0.079\cdot BW^{2/3}.$$

Spread and folded flipper areas (Fig. 2A) increased with body mass according to the following equations:

$$(12)\quad A_{\text{flip,spread}} = 0.030\cdot BW^{0.48}$$

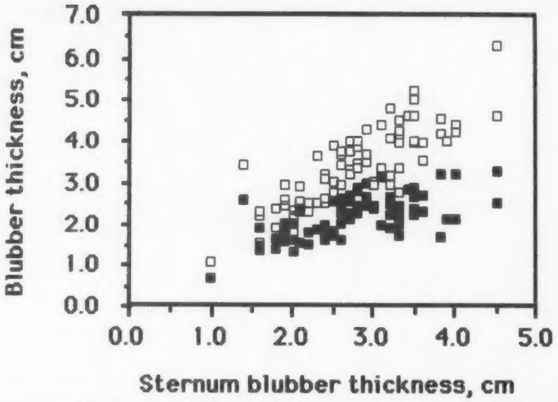

FIG. 5. Relationship of blubber thickness on the back (60% of standard length behind the snout) (☐) and neck (20% of standard length behind the snout) (■) to sternum fat depth.

$$(13)\quad A_{\text{flip,folded}} = 0.018\cdot BW^{0.49}.$$

Flipper area as a percentage of total area decreased with increasing body mass (Fig. 2B). Axial surface area (surface area excluding flippers, but including head) increased linearly with the square root of the product of body mass and length (Fig. 3, $r^2 = 0.96$). The regression line, forced through the origin (Snedecor and Cochran 1967), is given by

$$(14)\quad A_{\text{body}} = 0.112\cdot\sqrt{BW\cdot L}.$$

Data for fin and sei whales (including foetuses), calculated from data given by Lockyer and Waters (1986), are shown in the inset along with the graph of eq. (14). Correcting for blood loss did not change the regression line.

Blubber Distribution

Blubber thickness increased towards the middle of the body. The blubber was thickest on the back, about 60% of total length behind the snout (Fig. 4). Blubber thickness at any site was linearly related to sternum fat depth (Fig. 5), although the correlation was generally poorer on the neck and head than on the rest of the body. On the head and neck, the blubber layer was thickest ventrally; posterior to the fore flippers, it was thickest dorsally. Mean blubber thickness was also greatest slightly behind the middle of the body (Fig. 6). The ratio of thickness to radius varied less than thickness itself (Fig. 6). In immature animals, and in mature animals shot before the middle of May, the thickness to radius ratio increased in the hind part of the body. In immature animals, blubber thicknesses over the body were about 20% less in June than in April. In mature animals, blubber thickness decreased all over the body, 15–20% in the head and neck region, rising to 40% in the hind part (Fig. 6 and 7).

Equivalent Thickness and Insulation

The equivalent thickness was on average 50% larger than mean blubber thickness; the ratio d_{eq}/d_{mean} was 1.49 ± 0.15 (mean ± SD). Using equivalent thickness in eq. (10), the calculated cooling rate (*b*) was not significantly different ($p > 0.05$) from that measured (Fig. 8; Table 1). Using the measured blubber thickness, the calculated cooling rate was $12.7 \pm 2.4\%$ higher than that calculated from d_{eq}, and it was sig-

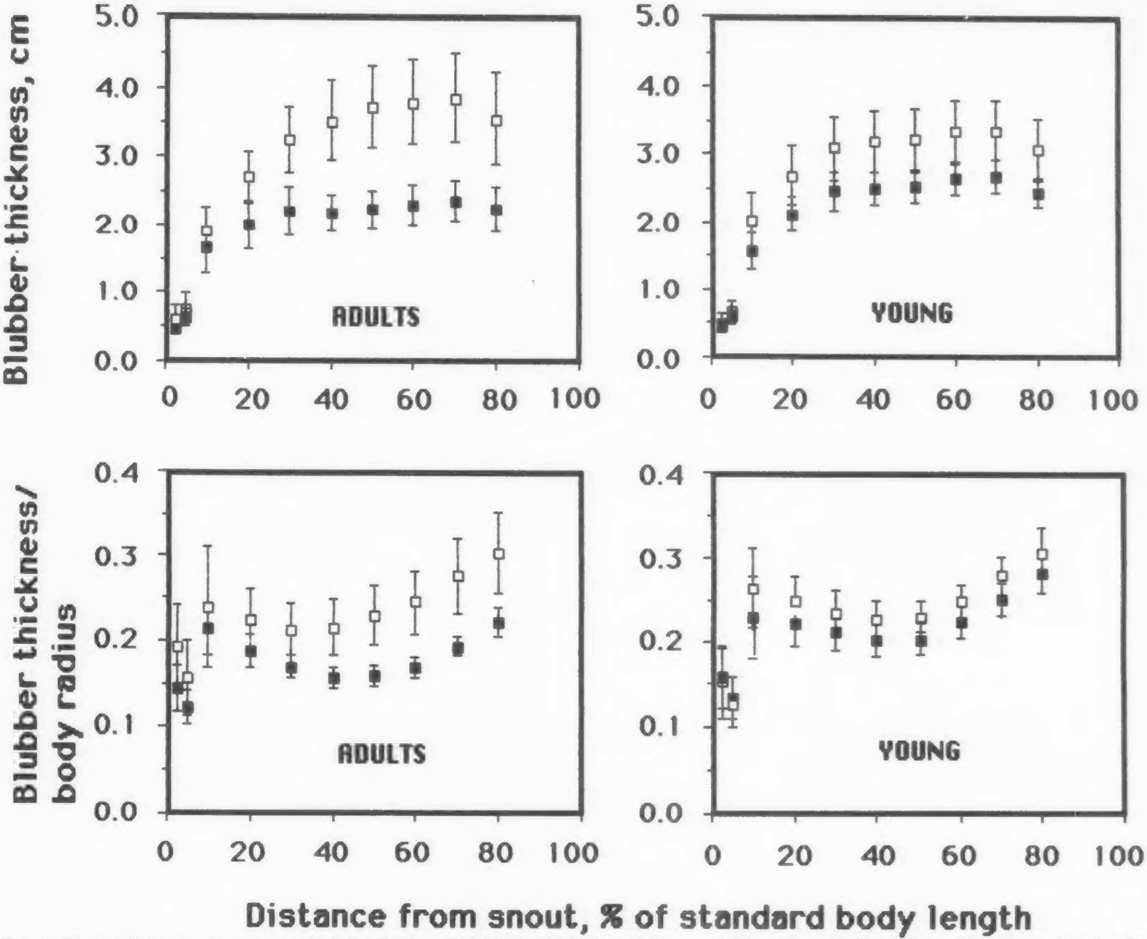

FIG. 6. Seasonal changes in topographical distribution of blubber and blubber thickness to body radius ratio in mature and immature ringed seals. □, before 15 May; ■, after 15 May.

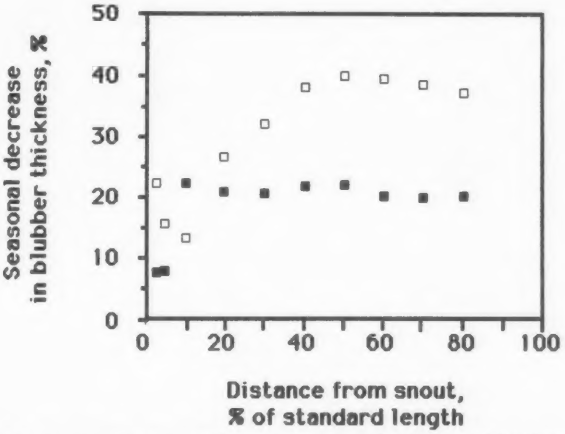

FIG. 7. Topographical differences in seasonal decrease of blubber thickness in mature (□) and immature (■) seals.

nificantly ($p < 0.005$) higher than the measured cooling rates (Fig. 8; Table 1).

Equivalent thickness was a linear function of the product of the absolute value of $\log_e(\mathrm{BW/LBW})$ and $\sqrt{\mathrm{BW}/L}$ (Fig. 9, $r^2 = 0.88$). The regression line, forced through the origin, is given by

$$(15)\quad d_{\mathrm{eq}} = 0.0098\sqrt{\mathrm{BW}/L}\cdot\log_e(\mathrm{BW/LBW}).$$

The regression coefficient remained the same (0.0098) when body mass was corrected for 10% blood loss, skin was included in blubber thickness, and lean body mass was replaced with core mass. For 15% blood loss, it increased to 0.0099. Data for sei and fin whales, calculated from data in Lockyer and Waters (1986), are shown in the inset along with the graph of eq. (15).

By substituting the expressions in eq. (14) and (15) for A and d in eq. (5), one arrives at the following expression for calculating minimum heat loss from the body of marine mammals:

$$(16)\quad H_{\min} = \frac{11.4\cdot k\cdot L\cdot \Delta T}{\log_e(\text{body mass/core mass})}.$$

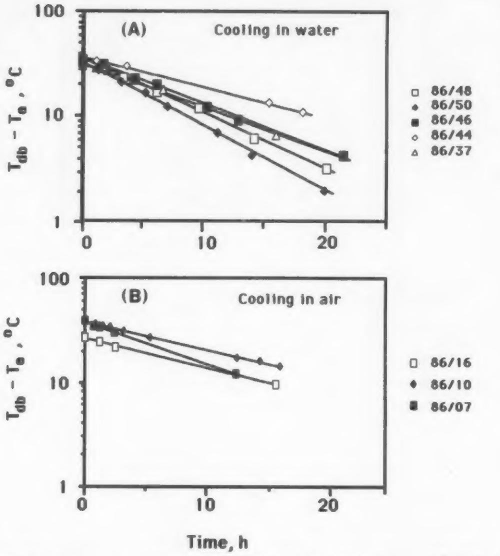

FIG. 8. Postmortem cooling of ringed seals in (A) water and (B) air.

Discussion

Surface Areas

The relationship between body mass and total surface areas described here is not significantly different from that described by Irving et al. (1935) and Iversen and Krog (1973) ($A_{total} = 0.08 \cdot BW^{2/3}$). The disadvantage with this (Meeh's) relationship is that, although the exponent 2/3 supposedly holds for all species, the constant depends on shape. For calculations of heat loss through the body surface, one also must subtract flipper areas, which are quite variable, even within the species (Fig. 2). The data presented in Fig. 3, along with the rationale for testing this relationship, suggests that eq. (14) is an alternative way of computing axial surface area.

Blubber Distribution

The heat loss equation for a cylindrical body (eq. (6)) can be rewritten $H = -2\pi kL\Delta T/\log_e(1-d/r)$. From this form of the equation, it is evident that the heat loss per unit length of a cylinder does not depend on the wall thickness per se, but on the ratio between wall thickness and the radius of the cylinder. By differentiating the heat loss equation for two cylindrical elements with respect to the wall thickness to radius ratio in one of the elements, it can be shown that the blubber distribution that gives the lowest heat loss is one where the ratio of blubber thickness to body radius is constant. It is evident from Fig. 6 that the d/r ratio is much less variable than blubber thickness itself. Although the d/r ratio is less on the head than on the rest of the body, the insulation is not as poor as might be expected from its thin blubber layer. Still, there are topographical differences. In sexually immature animals, and in adults in spring, the hind part of the body has the highest d/r ratio, and is consequently "overinsulated." When the animal loses fat, it has the least effect thermally if it is lost from this "overinsulated" hind part. Such a pattern of fat loss is indeed seen from April to June in the sexually mature animals (Fig. 6 and 7), which lose more mass than the immature animals during this period (M. Ryg, T. G. Smith, and N. A. Øritsland, unpubl. data). The pattern of blubber loss described above is probably what is reflected in the inuit word "sierkolik," meaning an animal with prominent hips (actually knees), and denoting a seal in poor condition (McLaren 1958). McLaren and Smith (1985) pointed to the inadequacy of existing indices of nutritional condition. An index based on measurements in the hind part of the animal, where variability is greatest, might be preferable. This is similar to the suggestion of Lockyer and Waters (1986) and Lockyer et al. (1985) of basing an estimate of body mass in whales on the girth 55–57% of body length behind the snout because this was the region of maximum variability.

A compromise between streamlining and insulation could also be involved in determining the pattern of blubber distribution, since increasing the maximum radius increases water resistance. Keeping blubber away from the thickest part of the body would be advantageous in reducing drag. In the mature animals the least blubber was lost on the neck; the d/r ratio in this area remained almost constant during the period of mass loss.

Equivalent Thickness and Insulation

As pointed out in the Methods section, the relationship between equivalent thickness and $\sqrt{BW/L} \cdot \log_e(BW/LBW)$ might be expected to be linear, and independent on size and shape. This seems to hold in practice — the values calculated for equivalent thickness from the data of Lockyer et al. (1985) for fin and sei whales are close to the regression line calculated

TABLE 1. Observed and calculated postmortem cooling rates[a] of ringed seals.

Animal No.	Radius (cm)[b]	C (J·kg^{-1})	d (cm)[c]	$b_{measured}$ ($10^{-5} \cdot s^{-1}$)	$b_{calculated}$ ($10^{-5} \cdot s^{-1}$) From d_{eq}	$b_{calculated}$ ($10^{-5} \cdot s^{-1}$) From d
86/50	11.8	3007	2.50	3.89	3.53	4.03
86/48	14.2	3143	2.04	3.30	3.42	3.74
86/46	13.7	3040	2.64	2.77	2.98	3.35
86/44	16.6	3085	2.84	1.84	2.20	2.45
86/37	14.5	3144	2.08	2.65	3.27	3.59
86/16	16.6	2954	3.92	1.80	1.71	1.97
86/10	14.7	3000	3.16	1.70	2.29	2.61
86/07	11.9	2960	2.81	2.64	3.21	3.71

[a] Logarithmic cooling rates (b in eq. (9) and (10)).
[b] Radius at site of temperature measurement equals the depth of the thermometer.
[c] Mean blubber thickness at the site of temperature measurement.

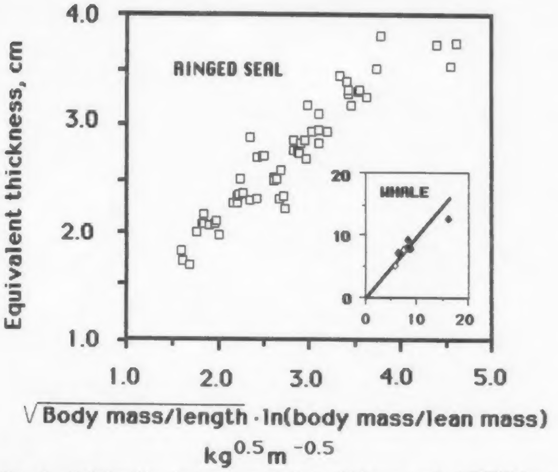

FIG. 9. Relationship between equivalent thickness and $\sqrt{BW/L}\cdot\log_e\cdot\sqrt{BW/LBW}$. □, *Phoca hispida*; ◆, *Balaenoptera physalus* (Lockyer and Waters 1986); ◇, *Balaenoptera borealis* (Lockyer and Waters 1986).

from the ringed seal data. It should be noted, however, that this linearity is empirical, not theoretical, since the equivalent thickness for the whole animal is calculated from the sum of the inverse values for each cylindrical element, and not as the actual mean of these values. In particular, the equation could be sensitive to differences in pattern of blubber distribution. Another source of error in the calculation of d_{eq} is the asymmetry in blubber thickness at each section (Fig. 4), which causes the calculated heat loss to be too low. It could be serious if there were large differences in blubber thickness at each cross section of an animal. However, calculated heat loss actually tended to be somewhat higher than measured heat loss, suggesting that the effects of such asymmetries were significant.

Using d_{eq} instead of d_{mean} for one cylindrical element (Table 1) only gives the effect on heat loss of cylindrical versus plane shape, whereas calculating d_{eq} for a whole seal also contains the effects of the distribution of blubber. Using the equivalent thickness for a single cylindrical segment instead of actually measured blubber thickness gave a better agreement with the measured postmortem cooling rates, but the difference between the two predictions was on average only 12.7%, as compared with the 50% difference between d_{eq} and d_{mean} found for whole animals. This indicates that the greater part of the difference between d_{eq} and d_{mean} for whole seals can be attributed to blubber distribution.

For a marine mammal that is exposed to temperatures below critical, i.e. it must increase its heat production to maintain homeothermy, eq. (16) should predict the heat production. Nordøy and Blix (1985) observed that the metabolic rate of fasting grey seal pups in ice water was about twice that in air. Body composition was measured with computed tomography, and body length can be estimated from the body masses using the equation length = $0.902 + 0.0045\cdot\text{mass}$ (Depuis 1982). Assuming a sculp mass of 50% of body mass and skin temperatures of 0°C, eq. (16) gives estimates of minimal heat loss of 2.9 and 4.0 $W\cdot kg^{-1}$ for the two animals, compared with the measured values of 2.6 and 4.2 $W\cdot kg^{-1}$. We believe that this is a reasonably good fit.

Since it is based on general physical laws (although simplified) and relationships that are independent of size and shape, we expect eq. (16) to hold for marine mammals in general. Since body length is a measure that is easy to obtain in the field, one is left with a need for a simple and reliable estimator for the mass of the body core, or alternatively, blubber and skin masses. A consequence of eq. (16) is that the minimal heat loss will not be affected by blubber loss as long as core mass is also lost, so that the body composition remains unchanged. Loss of core mass has been observed in fasting seal pups and suggested to have the function of sparing the blubber for insulation (Stewart and Lavigne 1980; Worthy and Lavigne 1983; 1987; Øritsland et al. 1985; Bowen et al. 1987). Core loss is especially pronounced in species such as the harp seal and hooded seal, where the postweaning fast often occurs in cold water (Worthy and Lavigne 1987). Equation (16) suggests that the importance of the mass loss from the core may not only be the amount of energy it contributes, but also that body composition is unchanged and heat balance maintained. This could explain why the metabolic rates of fasting harp seal pups in water increased only slightly, although they lost more than half of their blubber (Worthy and Lavigne 1987).

In conclusion, the blubber of ringed seals is distributed in such a way that the ratio of blubber thickness to body radius is nearly constant over the body, giving a near maximal insulation with a given amount of blubber. The hind part of the body has a somewhat higher thickness to radius ratio and is thus "overinsulated." The negative thermal effect of losing blubber during starvation can be minimized in two ways: by preferentially losing blubber from overinsulated parts of the body or by simultaneously losing substance from the body core. We give formulae for calculating body surface area and an *equivalent blubber thickness* for calculations of heat loss. Finally, by combining these equations, we suggest a general formula for calculating a lower limit for heat loss from marine mammals.

Acknowledgements

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Relative Selectivities of Miller High-Speed Samplers and Light Traps for Collecting Ichthyoplankton

R. S. Gregory[1] and P. M. Powles

Department of Biology, Trent University, Peterborough, Ont. K9J 7B8

Gregory, R. S., and P. M. Powles. 1988. Relative selectivities of Miller high-speed samplers and light traps for collecting ichthyoplankton. Can. J. Fish. Aquat. Sci. 45: 993–998.

Comparative studies on the relative selectivities of Miller high-speed samplers and light traps in Chemung Lake, Ontario, were made over 29 "site-nights" from May 13 to June 25, 1982. Yellow perch (*Perca flavescens*), Iowa darter (*Etheostoma exile*), and pumpkinseed sunfish (*Lepomis gibbosus*) constituted 97.2% of the 4376 specimens collected. A percent similarity index indicated a high uniformity in the size and species composition of the catch (~70% for much of the study); similarity was least on the earliest sample date (May 13, 3.5%). Smaller darters (<6.0 mm total length) were excluded from the Miller sampler catch. We suggest that extrusion of prolarval and early postlarval darters through the tow nets is responsible for low percent similarity index values in early May. We propose that investigators consider a mixture of passive and active sampling techniques to alleviate existing selectivity biases.

On a mené des études comparatives sur la sélectivité relative des échantillonneurs à grande vitesse de Miller et des pièges lumineux au lac Chemung (Ontario) utilisés la nuit à 29 emplacements du 13 mai au 25 juin 1982. La perchaude (*Perca flavescens*), le dard à ventre jaune (*Etheostoma exile*) et le crapet-soleil (*Lepomis gibbosus*) constituaient 97,2 % des 4 376 spécimens recueillis. Un indice de similarité des pourcentages indiquait qu'il y avait une grande uniformité de la taille et de la composition des espèces dans les prises (~ 70 % pour une bonne partie de l'étude); la similarité était la moins grande à la date la plus précoce de prélèvement d'échantillons (13 mai, 3,5 %). Les dards petits (longueur totale <6,0 mm) ont été exclus des prises réalisées avec l'échantillonneur de Miller. Nous émettons l'hypothèse que le passage de dards avant le stade larvaire et au début du stade post-larvaire à travers les filets traînants explique les faibles valeurs de l'indice de similarité des pourcentages enregistrées au début de mai. Nous proposons que les chercheurs envisagent un mélange de techniques d'échantillonnage passives et actives pour atténuer les erreurs de sélectivité existantes.

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Effectiveness of sampling gear is an important issue in ichthyoplankton research. Comparative studies between various larval fish sampling devices are numerous (Cole and MacMillan 1984; Freeman et al. 1984; Gallagher and Conner 1983; LaBolle et al. 1985; Madenjian and Jude 1985; Thayer et al. 1983 are several of the most recent). Two features commonly emerge from these investigations: (1) in reporting data, the numerical abundance in the catches is often disproportionately emphasized and the size of individuals receives secondary treatment and (2) the devices investigated tend to be all of one general type, usually "active" methods involving water passage through a mesh (e.g. towing, pumping, pushnets, etc.). Direct comparisons of such gear with "passive" techniques (e.g. drop boxes, fry traps, light traps, etc.) are rare, although the latter have been shown to be effective samplers (Freeman et al. 1984; LaBolle et al. 1985).

The present study compares the relative selectivity of an active (Miller high-speed sampler) and a passive (light trap) method of collecting ichthyoplankton. In Chemung Lake, Ontario, the former can be used only in early spring before extensive macrophyte growth occurs. Weeds and obstructions (e.g. stumps, rocks, etc.) can exclude the use of Miller samplers in other lakes. The use of light traps is not restricted by such obstructions. Miller samplers (Miller 1961) are commonly employed in larval fish surveys, but light traps are a relatively new device in ichthyoplankton collection (Paulson and Espinosa 1975). However, light traps have been used with increasing frequency since their introduction (Faber 1981, 1982; Floyd et al. 1984; Gregory and Powles 1985; Muth and Haynes 1984). In other areas of aquatic biology, light traps have been used for several decades (Baylor and Smith 1953; Hungerford et al. 1955; Kurien et al. 1952; Verheijen 1958).

The major criticism of the light trap has been one of species and size selectivity. This concern is justified, as the trap relies on the behavioural response of the individuals to light, which is subject to change during ontogeny (Bulkowski and Mead 1983; Girsa 1969; Verheijen 1958) or with light source intensity (Jones 1956; Woodhead 1956). Species that are attracted to a light trap at one size range may exhibit a photonegative response at another. This paper addresses the issue of species and size selectivity of the light trap by comparing it with concurrent catches of a Miller high-speed sampler.

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[1] Present address: Department of Zoology, The University of British Columbia, 6270 University Boulevard, Vancouver, B.C. V6T 2A9.

Methods

Study Area

Chemung (=Chemong) Lake lies approximately 6 km northwest of Peterborough, Ontario. Our study area, the south basin, is divided from the north end by a causeway 8.5 km from the extreme south end of the lake. The south basin has a maximum depth of 6.1 m (mean 1.8 m). The lake is uniformly shallow (generally 1–3 m), warm (22–27°C in July), and productive; the latter is due to agricultural runoff and the high degree of cottage and residential development. Macrophytes may occupy 430 ha (~50%) of the surface area by mid-June. A more complete description of the study area may be found in Gregory and Powles (1985).

Sampling Methods

Plexiglas light traps (hereafter referred to as traps) were slightly modified from the design of Faber (1981). Traps were constructed with one 95 × 50 mm external opening in each of the four sides, with the internal apertures set at 3.0 mm. The light source consisted of a 2.0-candlepower bulb powered by a 6-*V* dry cell battery. Sufficient styrofoam was added to ensure slightly positive buoyancy. More complete descriptions of the trap may be found in Faber (1981), Gregory (1983), and Gregory and Powles (1985). Traps were floated at the surface to a depth of 60 cm.

The Miller high-speed samplers (hereafter referred to as Miller samplers) were constructed of clear Plexiglas of 61 cm length and of 14 cm internal diameter; the diameter of the conical mouth was reduced to 10 cm. A No. 00 (0.70 mm) mesh was used throughout.

Four sites per evening were sampled at approximately 6-d intervals from May 13 to June 25, 1982 (except on June 5 and 25, when only three and two stations were sampled, respectively). This provided 29 "site-nights."

The sampling routine commenced 1.5 h after sunset to avoid the confounding effects of twilight illumination and continued for each site in turn (~2.5–3.0 h). Three traps were set and anchored in a line 15–20 m apart and allowed to fish for 20 min. Concurrently, two Miller samplers suspended 1 m laterally from the bow of a 5-m aluminum boat were towed in two complete elliptical paths at a distance of 15 m around the traps. Tow speed and depth were maintained at 7.5 km/h and 5–30 cm (measured from the top of the sampler), respectively. Flowmeter readings were used to determine the volume sampled. No significant disruptive effects of towing in the immediate vicinity of the traps were detected that would affect trap effectiveness (Gregory 1983).

Catches were preserved in 5% formalin and stored in sample bags in the field. Within 2 d, larvae were transferred to vials of 5% formalin buffered with sodium carbonate. Identifications were based primarily on Auer (1982) and Hogue et al. (1976). All larvae were counted and total lengths (TL) (to the nearest 0.01 mm) recorded. In cases of high catch, a randomly selected subsample of 30 larvae was measured.

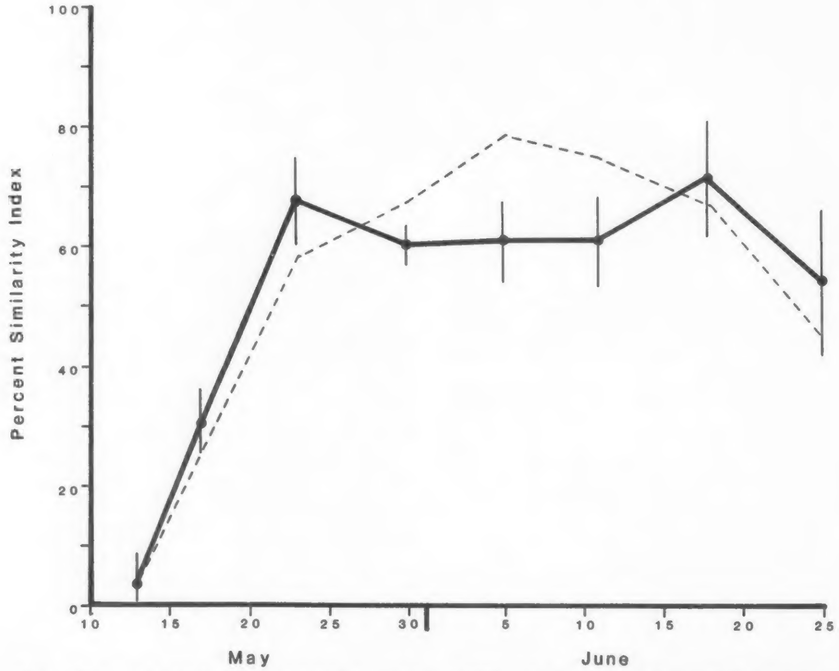

FIG. 1. Percent similarity index (± 1 SE) in catches of Miller high-speed samplers and light traps in Chemung Lake, Ontario, during May and June 1982 (solid line = mean of all sites, broken line = pooled by date).

TABLE 1. Mean total lengths and catches of Miller high-speed samplers and light traps in Chemung Lake, Ontario, 1982 (1 = number measured, 2 = number caught, 3 = density in numbers/m^3; *mean TL's significantly different ($p < 0.05$)).

		Miller sampler					Light trap			
			N					*N*		
Species	Date	$\bar{X}$ TL (SD) (mm)	1	2	3	% prolarvae	$\bar{X}$ TL (SD) (mm)	1	2	% prolarvae
Yellow perch	May 13	8.3 (0.7)	99	112	4.4	22	8.3 (0.4)	8	8	38
	May 17	10.8 (0.9)	176	388	8.4		11.0 (0.9)	24	24	
	May 23	13.1 (1.2)	188	827	19.3		13.2 (1.0)	141	202	
	May 30	15.7 (1.4)	104	132	3.2		16.9 (1.2)	183	234	
	June 5	18.8 (1.7)	21	22	0.8		19.1 (1.4)	29	30	
	June 11	21.1 (1.4)	6	6	0.3		20.2 (1.7)	59	60	
	June 18	25.6 (2.5)	9	9	0.3		25.8 (1.4)	93	134	
	June 25	29.8	1	1	0.1		27.9 (1.7)	27	27	
Iowa darter	May 13*	6.8 (0.2)	2	2	0.1		4.7 (0.7)	171	292	58
	May 17*	7.7 (1.0)	29	29	0.6		5.3 (1.5)	86	87	55
	May 23*	9.7 (1.5)	69	92	2.2		8.7 (2.7)	133	204	13
	May 30	9.8 (1.7)	31	31	0.8		10.6 (2.1)	188	119	2
	June 5*	10.3 (2.3)	15	15	0.6		12.8 (3.1)	30	30	
	June 11	11.5 (2.7)	9	10	0.5		11.6 (2.2)	55	56	4
	June 18	11.9 (0.5)	3	3	0.1		11.8 (1.6)	8	8	
	June 25						13.4 (1.6)	3	3	
Pumpkinseed	May 13									
	May 17									
	May 23									
	May 30	6.2 (0.1)	2	2	0.1		5.7 (0.2)	2	2	50
	June 5	6.5 (0.3)	3	3	0.1		6.9 (0.5)	2	2	
	June 11	6.0 (0.6)	40	40	2.1	55	6.0 (0.5)	147	210	59
	June 18	6.4 (1.3)	31	31	1.1	68	6.1 (0.9)	180	540	75
	June 25*	8.7 (1.2)	9	10	0.7		7.5 (1.4)	26	26	19

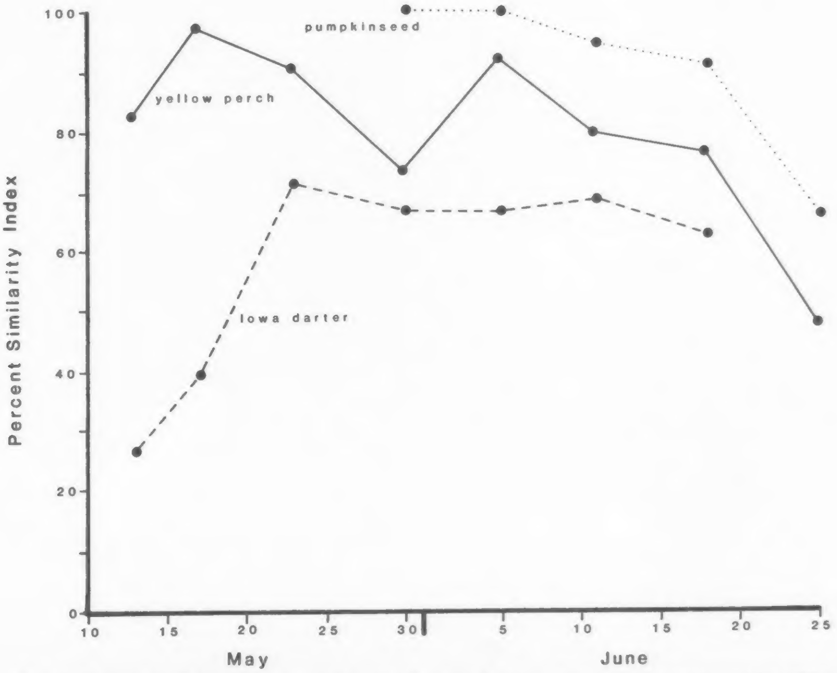

FIG. 2. Percent similarity index in catches of yellow perch, Iowa darter, and pumpkinseed by Miller high-speed samplers and light traps in Chemung Lake, Ontario, during May and June 1982.

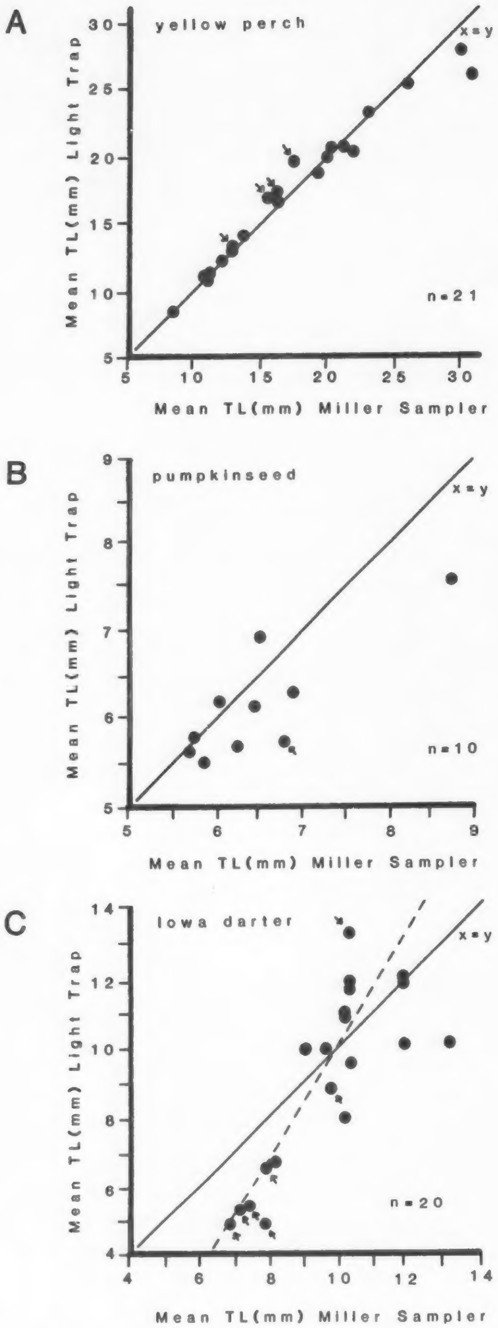

FIG. 3. Relationships between mean total lengths (TL) of yellow perch, pumpkinseed, and Iowa darter in concurrent catches of Miller high-speed samplers and light traps for all sites in Chemung Lake, Ontario, during May and June 1982 (arrows indicate points significantly different from unity, *t*-test, $p < 0.05$; broken line = the analytical relationship of the means in Fig. 3C).

Data Analysis

Statistical analysis (Student's *t*-test) indicated only occasional significant differences in the mean lengths of larvae caught by the same type of sampling device in any one site-night (i.e. among replicates). The number of significant differences was consistent with the probability of encountering Type I errors. On the strength of this analysis, data from all replicates of a sampling device were combined for each site-night.

To assess sampler selectivity, principal species were first segregated into 2.5-mm size classes. The size classes for each principal species, and all other species (irrespective of size class), were treated as separate categories (i.e. 28 total categories). We used a percent similarity index (Whittaker and Fairbanks 1958) to compare sampler catches. This index was also used to assess the similarities in the catches within individual species. A simple selectivity index (Strauss 1979) and Student's *t*-test were also used to compare catches.

Results

A total of 4376 larval specimens were taken from May 13 to June 25, 1982. Of these fish, 60.1, 24.5, and 12.6% were yellow perch (*Perca flavescens*), Iowa darter (*Etheostoma exile*), and pumpkinseed (*Lepomis gibbosus*), respectively. These percentages were not consistent between dates (see Table 1 for density estimates and catch). All other fish species contributed only 2.8% to the total sampled catch.

Few significant differences were detected in the mean lengths of yellow perch caught by the Miller sampler and the trap at individual sites, and these dissimilarities were slight. These were not reflected in the summarized data (Table 1). For pumpkinseed, a similar result was obtained with the exception of the final sampling date, when smaller mean lengths of sunfish were obtained by the traps. The Iowa darter, however, demonstrated a strikingly different pattern. The mean lengths of larvae of this species were less in the trap than in the Miller sampler throughout May (significant on May 13, 17, and 23; Table 1). This was also reflected by the total absence of yolk-sac-bearing Iowa darter larvae (=prolarvae) in the Miller sampler catches. By contrast, smaller darters were taken in abundance by the traps.

Early in the season, higher numbers of yellow perch were caught by the Miller sampler, compared with the trap, on each date (Table 1). This was not true of the Iowa darter or pumpkinseed, which were taken in higher numbers in the trap; respective peak catches were recorded in May and mid-June.

The trends described above indicated a seasonal change in both qualitative and quantitative aspects of the catches of the two sampling devices. Changes in the percent similarity index (Fig. 1) reflected the same seasonal trend. Selectivity index values (not shown) demonstrated that Iowa darter of smaller size classes (2.5–7.5 mm TL) were caught in low proportions in the Miller sampler relative to the trap. Early in the season, the similarity of the catches of the two devices was low (Fig. 1), being most dissimilar on May 13 (3.5%). Catch similarity rose until late May, when it stabilized at ~70% (pooled data exhibited a peak of ~80% in early June). Similarity decreased somewhat in late June. Mean catch similarity achieved a maximum of 71% on June 18 (Fig. 1), with catch similarity at one site attaining the season high of 91%.

Catch similarity between the Miller sampler and the trap for yellow perch was quite high (>70%) when the species was abundant in May (Fig. 2). The same was not true for Iowa darter. The percent similarity index for this species was lowest on May 13, with a mean of 31%, and increased to >70% by mid-May. Pumpkinseed appeared in late May with 100% similarity between the capture methods. The high initial percent similarity index value was probably due to the near uniform size of the newly emerged pumpkinseed larvae. Catches of the two samplers remained highly similar for this species throughout much of the remainder of the sampling season. The mean lengths of yellow perch and pumpkinseed collected by the two devices were similar (Fig. 3). Again, this was not the case for Iowa darter (Fig. 3C), where the relationship exhibited was a significant departure from unity ($p < 0.05$). The examination of individual species indicated that overall catch similarity was dependent upon that of the Iowa darter component.

Discussion

Greatest dissimilarity between total catches of the Miller sampler and the trap occurred in early May. This can be attributed to the between-sampler disparity in both the size of the Iowa darters and in the differential catch frequency of this species and yellow perch. However, one species caught in disproportionate numbers and sizes by one sampling method can give rise to a perception of apparent dissimilarity of the total catch of all species by any two samplers. We believe this to be the cause of the low catch similarity between the Miller sampler and trap during May. We base this conclusion predominantly on the strength of our similarity data with respect to the Iowa darter. There is a striking resemblance between the general pattern of similarity exhibited by the entire catch (Fig. 1) and that of the darter when examined in isolation (Fig. 2). This species represents a large proportion of the catches of both devices throughout much of the season, with the exception of May 13 and 17. On these dates, smaller Iowa darters seem to be selectively excluded from the catch of the Miller sampler, as evidenced by the complete absence of prolarval Iowa darter from this device. The most obvious explanation for the absence of smaller darters is their extrusion through the mesh of the towed sampler, as has been suggested in a number of other studies (Cole and MacMillan 1984; Thayer et al. 1983; Vannucci 1968). Although we did not observe partially extruded larvae in the nets, the presence of large numbers of *Chaoborus* larvae may have made them difficult to detect.

The increase in catch similarity between the two samplers after mid-May is probably due to the larger sized Iowa darter encountered after mid-May. Similarity increased to high levels in late May and early June. The late-season (i.e. after June 18) decline in similarity can be largely attributed to avoidance of the Miller sampler by larger size classes of yellow perch, which were caught in low numbers relative to the trap at this time. Explanations of similar effects are numerous in the literature (Cada and Loar 1982; Cole and MacMillan 1984; Gallagher and Conner 1983; Noble 1970; Thayer et al. 1983). The usual mitigating procedure is to increase towing speed. However, this merely shifts the inevitable avoidance effect to larger sizes and increases the probability of extrusion through the nets (Noble 1970; Thayer et al. 1983). Extrusion can be countered by reducing the mesh size (e.g. 0.25 mm). However, in eutrophic lakes such as Chemung, reduction in mesh size also results in rapid clogging of gear. A passive device could prove more effective in highly productive systems.

Comparisons of ichthyoplankton sampling gear have mostly been conducted using towed gear. Due to the inherent biases of any one device, we encourage the inclusion of several methodological types in sampling programs. Many previous authors have implied that multiple-device sampling should be implemented, but this has usually resulted in the use of several types of tow nets (e.g. bongo nets, Miller high-speed samplers, push nets, limnetic nets, etc.) or static nets (e.g. gill nets, seines, trap nets, etc.). Rarely have studies actually mixed types, usually relying on two or more representatives within the same general class of samplers, which often have similar inherent biases. Furthermore, when two types are mixed, it is rarely done for the purpose of augmenting the data gathered by other samplers, but rather for assessing abundance in different habitats or times of the season. The switching of gears is necessary to sample a wide range of specimen sizes and to follow ontogenetic shifts in behaviour, but should not be confused with the multiple-device sampling we are advocating.

By adopting methods that overlap in their applicability, the data collected will allow a more accurate evaluation of numerical and size composition of the ichthyoplankton. Researchers will be able to develop an enhanced picture of larval fish dynamics. We propose that the approach best suited to achieve this objective is to mix different methodologies and not to simply apply a variation of a single general method.

The size distribution of the ichthyoplankton is better represented using the light trap than the Miller high-speed sampler. Clearly, towed devices are better suited for quantitative ichthyoplankton collection, but valuable size range data are often suspect. The light trap may mitigate this deficiency when used in conjunction with Miller samplers and similar towed devices. Also, light traps and other passive devices are often the only way to sample physically obstructed, shallow, and highly productive systems.

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Interactions between Brook Charr, *Salvelinus fontinalis*, and Nonsalmonid Species: Ecological Shift, Morphological Shift, and Their Impact on Zooplankton Communities

Pierre Magnan

Département de chimie-biologie, Université du Québec à Trois-Rivières, C.P. 500, Trois-Rivières (Québec) G9A 5H7

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A quantitative survey of 26 oligotrophic Quebec lakes indicated that the presence of creek chub (*Semotilus atromaculatus*) or white sucker (*Catostomus commersoni*) had an impact on brook charr (*Salvelinus fontinalis*) populations. Evidence for competitive interactions among these species was provided by the observation that (1) the mean annual yield (kilograms per hectare) of charr was significantly reduced when they lived sympatrically with these species, (2) charr shifted their food habits from benthic organisms to zooplankton in the presence of creek chub and (or) white sucker, and (3) the length of the gill rakers of charr was significantly higher in lakes containing chubs and suckers. As the length of the gill rakers is reported to be correlated with the extent of plankton feeding, this latter result was interpreted as a morphological change associated with increased exploitation of zooplankton in sympatry. When occurring with creek chub, the niche shift of brook charr resulted in a significant change in zooplankton community structure. The proportion of large zooplankton organisms (>1.1 mm) declined whereas that of the smaller ones (<0.6 mm) increased. Also, the mean length of *Holopedium*, the larger cladocerans, was significantly reduced in sympatric creek chub – charr lakes compared with lakes where charr lived allopatrically. A similar impact on zooplankton was not as clear when charr occurred with white sucker. When living with white sucker, brook charr populations appeared to be sufficiently reduced as to have little or no effect on zooplankton communities.

Un inventaire quantitatif de 26 lacs oligotrophes du Québec a indiqué que la présence du mulet à cornes (*Semotilus atromaculatus*) ou du meunier noir (*Catostomus commersoni*) avait un impact sur les populations d'ombles de fontaine (*Salvelinus fontinalis*). Les évidences d'interactions compétitives entre ces espèces ont été fournies par l'observation 1) que le rendement annuel moyen (kilogrammes par hectare) des ombles était significativement réduit lorsqu'ils vivaient en sympatrie avec ces espèces, 2) que les ombles changeaient leur niche alimentaire du zoobenthos au zooplancton en présence du mulet à cornes et (ou) du meunier noir et 3) que les peignes branchiaux des ombles étaient significativement plus longs dans les lacs contenant du mulet et du meunier. Comme il est reconnu que la longueur des peignes branchiaux est corrélée à l'importance des organismes planctoniques dans l'alimentation des poissons, ce dernier résultat a été interprété comme un changement morphologique associé à une plus grande exploitation du zooplancton en sympatrie. En présence du mulet à cornes, le déplacement de niche des ombles de fontaine se traduisait par un changement significatif de la structure des communautés zooplanctoniques. La proportion des grands organismes zooplanctoniques (> 1,1 mm) diminuait alors que celle des plus petits (< 0,6 mm) augmentait. De plus, la longueur moyenne de *Holopedium*, le plus grand des cladocères, était significativement réduite dans les lacs contenant du mulet à cornes et de l'omble de fontaine, comparativement aux lacs contenant seulement de l'omble de fontaine. Un impact similaire sur le zooplancton n'a pas été aussi clair dans les lacs où l'omble de fontaine était retrouvé avec le meunier noir. Les populations d'ombles de fontaine semblaient suffisamment réduites dans ces lacs pour avoir peu ou pas d'effet sur les communautés zooplanctoniques.

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Evidence that interspecific competition occurs in nature is provided when the niche shift of a resident species is caused by the introduction of a second species (Diamond 1978; Werner 1986), when a character displacement is observed (Brown and Wilson 1956), or when it is demonstrated that a resource, such as food, is in short supply (Diamond 1978; Sale 1979; Hanson and Leggett 1986). If interspecific competition is important, one also expects a reduction in the number of individuals or in the total biomass of the resident species in the presence of an introduced species (Werner 1986). Although niche shift has been well documented in different systems (Diamond 1978; Werner 1986), there are very few examples of character displacement (Crowder 1984; Schluter et al. 1985), of a limiting resource (Lammens et al. 1985; Hanson and Leggett 1986), or of one species reducing the number or biomass of another species (Werner 1986).

Creek chub (*Semotilus atromaculatus*) and white sucker (*Catostomus commersoni*) have been introduced by bait fishermen in many brook charr (*Salvelinus fontinalis*) lakes of Quebec and may naturally overlap in distribution with charr (Scott and Crossman 1973). There is evidence that these species can force brook charr to shift their food habits from benthic organisms to zooplankton in some oligotrophic lakes (Magnan and FitzGerald 1982, 1984; S. Tremblay and P. Magnan, in prep.). The first objective of the present study was to determine whether this change in diet causes morphological changes in charr. Lindsey (1981) and Crowder (1984) provided evidence that the number and the length of gill rakers in two *Coregonus* species can change in the presence of more specialized zooplankton feeders. Long and numerous gill rakers are related to zooplankton feeding, and changes in these characteristics can occur over a relatively short period of time (within 10 yr in Coregonidae; Lindsey 1981). As the presence of creek chub and white sucker has been reported for at least 25 yr in the study lakes, it is plausible that changes in gill raker structure of brook charr may have occurred during their shift to zooplankton.

A second objective of the study was to determine whether the niche shift of sympatric brook charr affects zooplankton communities. The observation of such an effect provides evidence of resource limitation in lake fish communities (Werner 1986). The impact of fish on zooplankton community structure has been documented (Hrbacek et al. 1961; Brooks and Dodson 1965; Galbraith 1967; Zaret 1980; Spencer and King 1984; Scavia et al. 1986; Vanni 1986). The global conclusion of these studies was that fish predation resulted in a reduction of large zooplanktonic organisms which were replaced by smaller ones. However, almost all of these studies focused on the impact of planktivorous fish on the abundance, composition, and size structure of zooplankton communities. Very few studies have considered the possibility that an omnivorous fish such as brook charr could affect the zooplankton in the same way as more specialist feeders on zooplankton (i.e. planktivores).

A third objective of this study was to determine whether the presence of creek chub and (or) white sucker diminishes the production of brook charr populations. To investigate these questions, I compared 10 lakes containing allopatric brook charr populations, 8 lakes containing brook charr and creek chub, and 8 others where brook charr lives sympatrically with white sucker.

Studied Lakes

The 26 studied lakes were located in the Mastigouche Reserve, just north of Trois-Rivières (Québec) (46°40′N,

TABLE 1. General characteristics of the studied lakes containing allopatric and sympatric brook charr populations.

Lake	Surface area (ha)	Mean depth (m)	Conductivity (μS/cm)	Secchi disk (m)	Other fish species[a]				Samples[b]		
					PO	SA	CCo	SM	SC	GR	ZOO
Allopatric											
Bondi	23.3	8.0	10.5	3.5	×				×		×
Cerne	10.4	4.4	10.7	2.6	×				×	×	×
Charme	18.1	3.2	9.2	3.7	×				×	×	×
Chute noire	18.1	3.4	12.1	4.3	×					×	
Diablos	7.8	2.9	10.5	3.7	×						×
Leonard	13.0	12.6	9.8	3.7	×				×		×
Osborn	7.8	4.8	12.0	3.4	×				×		×
Petit	8.0	1.1	10.7	3.6						×	
Simpson	28.5	3.3	12.5	2.5					×		×
Vautour	7.3	4.8	12.5	3.6	×				×	×	×
Creek chub											
Bourgeois	14.2	5.9	13.8	2.7	×	×			×		×
Daniet	21.0	4.6	10.0	2.7	×	×			×	×	×
French	3.0	2.4	14.2	1.8	×	×				×	
Grosse	6.2	6.2	15.5	2.6	×	×					×
Petit Carufel	10.4	6.2	15.6	4.3		×			×	×	×
Rose	11.4	4.8	15.5	3.0		×		×	×		×
Tête	18.1	2.4	12.4	2.9	×	×			×	×	×
Vertnez	38.8	11.9	19.4	4.0		×			×		×
White sucker											
Brise	33.7	2.3	9.8	2.4	×	×	×				×
Grignon	25.9	7.8	9.0	5.5	×		×	×	×		×
Jimmy	35.0	2.6	14.2	2.5	×	×	×		×		×
Joie	10.4	6.5	8.7	3.0			×		×	×	×
Jones	26.3	7.6	13.5	4.6	×	×	×				×
Sauterelle	7.5	5.3	11.2	4.5	×		×	×	×	×	×
Sans-nom	13.2	0.8	12.7	1.5			×			×	
Vert	15.5	7.6	11.2	6.7	×	×	×		×	×	×

[a] PO, northern redbelly dace (*Phoxinus eos*); SA, creek chub (*Semotilus atromaculatus*); CCo, white sucker (*Catostomus commersoni*); SM, pearl dace (*Semotilus margarita*).

[b] SC, charr stomach contents; GR, charr gill rakers; ZOO, zooplankton.

73°20′W). These lakes were typical of small oligotrophic temperate zone lakes with respect to surface area, mean depth, conductivity, thermal stratification, and Secchi disk transparency (Table 1). Summer concentration of O_2 ranged typically from 9.2 to 12.8 ppm at the water surface of other lakes of the same area (Magnan 1982). As the lakes were located close together (1500 km^2), they were exposed to similar climatic conditions. All lakes were subject to sport fishing, and exploitation was carefully controlled by the Québec government.

The lakes were divided into three groups that will be referred to hereafter as (1) "allopatric lakes" containing brook charr with or without northern redbelly dace (*Phoxinus eos*), (2) "creek chub lakes" containing brook charr and creek chub with or without northern redbelly dace and pearl dace (*Semotilus margarita*), and (3) "white sucker lakes" containing brook charr and white sucker with or without northern redbelly dace, pearl dace, and creek chub (Table 1). Almost all lakes contained *P. eos* (Table 1), but their presence did not affect significantly the mean yield of brook charr in the exploited lakes of the Mastigouche Reserve (P. Magnan, unpubl. data). Also, gillnet fishing realized in three of the white sucker lakes (Grignon, Sauterelle, and Vert) indicated that the relative biomass of *S. atromaculatus* and *S. margarita* represented less than 1% of the total fish biomass in these lakes. Although not quantified, the same should be true for *P. eos*. Thus, my descriptive classification of the three lake types is representative of the species present for the purpose of this study.

Materials and Methods

Fishing data

To determine whether the introduced species had an effect on the production of brook charr, I compared the mean charr yield among allopatric, creek chub, and white sucker lakes. For each lake, the Ministère du Loisir, de la Chasse et de la Pêche du Québec, provided data on the annual yield (kilograms per hectare) of brook charr since 1972. In 1972, the yield of each lake was set arbitrarily to 4.5 kg/ha. Afterwards, it was adjusted yearly up to the reach of a maximum sustainable yield (Ricker 1975) in equilibrium with a given fishing success (1 fish/ha) (Benoît 1982). I then computed a mean yield for each studied lake (from 1972 to 1985) and used these data to compute a mean yield for each group of lakes.

Food Habits of Brook Charr

To determine whether the presence of creek chub and white sucker affected the food habits of brook charr, stomach contents of charr sampled in seven allopatric lakes, six creek chub lakes, and five white sucker lakes were studied (Table 1). Stomach contents were obtained from brook charr captured by sport fishermen (during daylight periods) between July 23 and August 4, 1985. Stomachs were immediately removed following capture and placed in a 5% formaldehyde solution. The part of the digestive tract that was situated between the oesophagus and the pyloric valve was analysed. Wet weights (± 1.0 mg) of zooplankton, of benthic organisms, and of other foods (fish and terrestrial insects) were recorded. For each brook charr population, the data were expressed as the mean percent weight of each food category found in the stomach contents (Wallace 1981; Walsh and FitzGerald 1984). More detailed studies of the food habits of brook charr in these systems may be found in Magnan and FitzGerald (1982) and S. Tremblay and P. Magnan (in prep.).

Gill Raker Structure of Brook Charr

The gill raker structure of brook charr was studied in five allopatric lakes, four creek chub lakes, and four white sucker lakes (Table 1) on a minimum of 10 fish per lake. Samples were obtained between July 23 and August 4, 1985, from captures by sport fishermen. The number of gill rakers was counted on the first gill arch, and the length of the longest gill raker was measured at the bend of the first gill arch, using an ocular micrometer.

Zooplankton Communities

The zooplankton communities were investigated in eight allopatric lakes, seven creek chub lakes, and seven white sucker lakes (Table 1) between July 15 and 19, 1985. Zooplankton was collected at three stations in the central part of the lakes. At each station, a vertical haul was made from a 10-m depth to the surface using a 12-cm-diameter Wisconsin plankton net with 80-μm mesh size. When the maximum depth was less than 10 m (on five of the 22 lakes) the hauls were made from 0.5 m of the bottom. The number of organisms found in these samples was standardized for 10-m hauls. Samples were preserved in a 95% ethanol solution. In each lake, the water transparency was measured using a 20-cm Secchi disk.

In the laboratory, all cladocerans of each sample were identified to genera and measured to the nearest 0.01 mm using a Wild dissecting microscope and an ocular micrometer. Other taxa such as copepods were not considered in this study because they were rarely found in the stomach contents of the fish. The length of the cladocerans was measured from the top of the head, or the base of the helmet if present, to the base of the tail spine (Lammens et al. 1985). Zooplankters were grouped in three size classes for statistical analysis: <0.6 mm, 0.6–1.1 mm, and >1.1 mm. These classes corresponded to well-separated intervals in the overall size frequency distribution of the 22 studied lakes (Fig. 1).

The data were expressed as the number of organisms per cubic metre to account for zooplankton abundance and as the percent of each group to account for zooplankton community structure (see Evans 1986). The latter was necessary because of the comparison of different sample sizes of each lake. In this paper, all interpretations will be based on the total sample taken in each lake (i.e. on the summation of the three hauls).

Statistical Analysis

For each parameter, differences among lake types (i.e. allopatric, creek chub, and white sucker) were investigated with an ANOVA followed by a Student–Newman–Keuls multiple-range comparison test. A modified Ryder's index (Ryder et al. 1974) was also computed (conductivity/mean depth) to determine whether the lake types were comparable in this respect. Because the assumptions of normality and homogeneity of variances were generally not met, the analyses were performed on transformed data. Frequency data were log $(x + 1)$ transformed and proportions were arcsine-square root transformed. The homogeneity of variances were tested with an F_{max}-test and the normality was tested with a Kolmogorov–Smirnov test (Sokal and Rohlf 1981). The gill raker structure data of brook charr were analysed with an ANCOVA (Sokal and Rohlf 1981) to remove

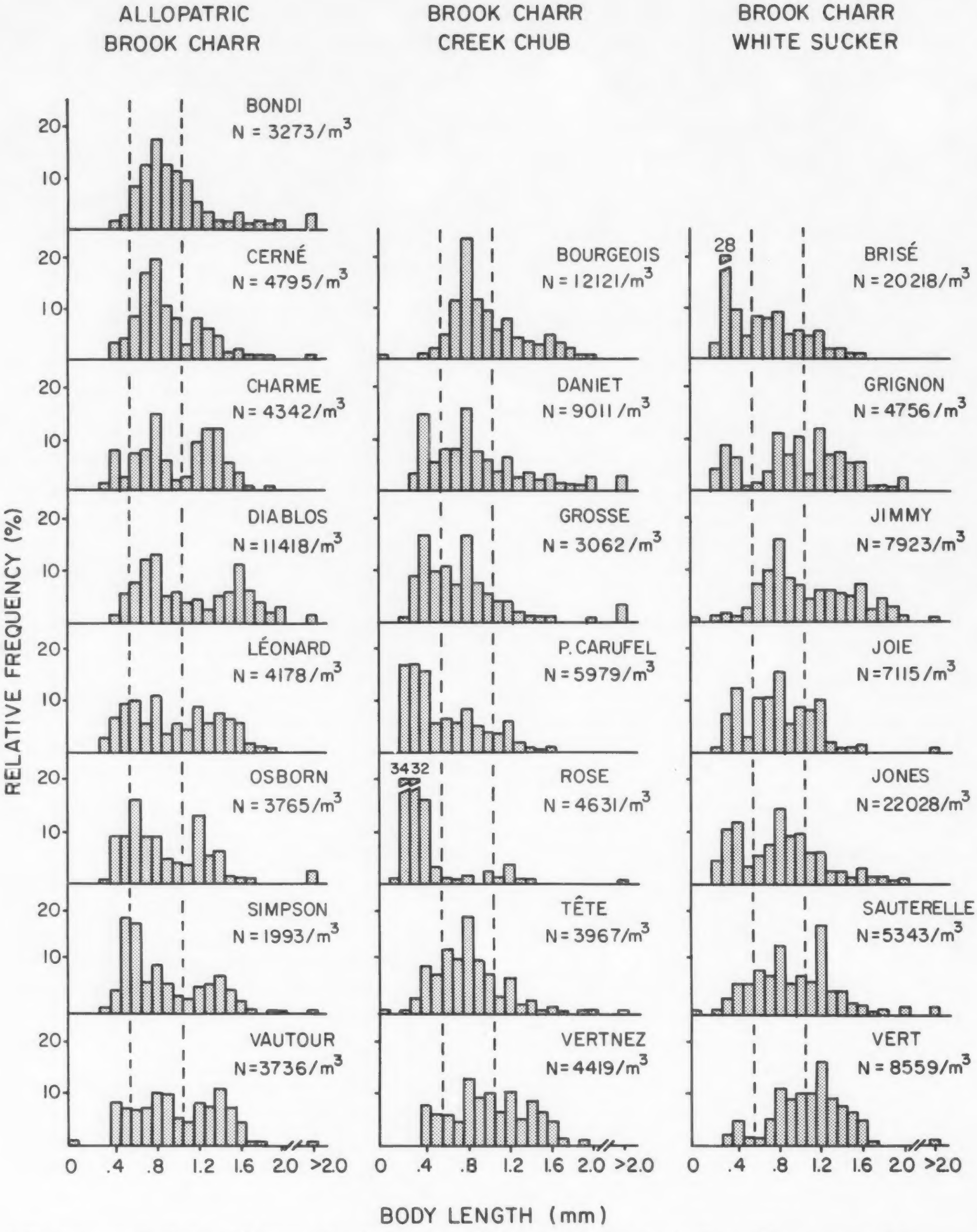

FIG. 1. Size frequency distribution of cladocerans found in the 22 studied lakes. Statistical tests for significant differences among fish communities are given in Table 2. Broken lines indicate the size classes used in statistical analyses.

the effect of body size on these meristics. The variables (number and length of the gill rakers) as well as the covariable (total length) were log $(x + 1)$ transformed before analyses. The differences among the adjusted means were determined using the approximate comparison intervals method of Gabriel (Sokal and Rohlf 1981).

Pearson product-moment correlation coefficients were determined between the characteristics of the lakes and the response variables (i.e. brook charr yield and zooplankton data) in order to determine whether any differences in these characteristics would explain the response variables. Each variable was transformed as mentioned above before the analyses to meet the assumption of normality underlying this model. Because the probability of making a Type I error is equal to $p < 0.05$ in the same family of tests (i.e. tests that use the same set of observations), the Bonferonni technique was used in assigning significance to the correlation coefficients (e.g. Gatz 1979). Each individual test was then conducted at a probability of $0.05/n$, where n is the number of tests in the same family, giving a value of 0.01 in this study.

Results and Discussion

Lake Characteristics

There were no significant differences in the characteristics of the lakes with the exception that conductivity was significantly higher in the creek chub lakes than in the allopatric and white sucker lakes (Table 2). This result might suggest a higher productivity of the creek chub lakes (see Ryder et al. 1974). However, I observed no significant differences in the modified Ryder index among the three groups of lakes (Table 2).

TABLE 2. Results of ANOVA's for significant differences in studied parameters among fish communities. Data are means (± 1 SD in parentheses). Means followed by different letters are significantly different as determined by a Student–Newman–Keuls multiple-range comparison test. Note: Actual data are presented here but analyses were performed on transformed data (see text).

Parameter	Allopatric brook charr	Brook charr creek chub	Brook charr white sucker	df	*F*	*p*
			Lake characteristics			
Surface area (ha)	14.2 (7.5)	15.0 (10.3)	20.9 (10.7)	2;23	1.17	NS
Mean depth (m)	4.9 (3.3)	5.6 (3.0)	5.1 (2.8)	2;23	0.20	NS
Conductivity (μS/cm)	11.1 a (1.2)	14.6 b (2.7)	11.3 a (2.1)	2;23	7.20	<0.01
Modified Ryder's index	3.3 (2.4)	3.2 (1.5)	4.1 (4.8)	2;23	0.05	NS
Secchi disk transparency (m)	3.5 (0.5)	3.0 (0.8)	3.8 (1.8)	2;23	0.79	NS
			Fishing data			
Brook charr yield ($\text{kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$)	5.3 a (1.1)	3.6 b (1.6)	2.9 b (0.6)	2;23	9.30	<0.001
			Feeding habits of brook charr (mean % weight)			
% zooplankton	45.7 (21.1)	44.9 (27.4)	73.5 (14.2)	2;15	2.91	NS
% zoobenthos	47.2 a (21.6)	42.1 a (21.4)	15.8 b (15.9)	2;15	4.81	<0.02
			Zooplankton community structure (% of total no. of cladocerans)			
Small cladocerans (<0.6 mm)	14.5 (7.3)	34.5 (28.2)	21.7 (13.5)	2;19	2.15	NS
Intermediate cladocerans (0.6–1.1 mm)	46.3 (10.7)	41.4 (18.8)	41.8 (7.0)	2;19	0.39	NS
Large cladocerans (>1.1 mm)	39.2 a (7.9)	24.1 b (12.9)	36.5 ab (14.1)	2;19	3.65	<0.05
Bosmina	2.2 (1.5)	19.2 (29.5)	14.0 (11.3)	2;19	2.50	NS
Daphnia	56.2 (18.7)	43.3 (31.2)	60.5 (14.1)	2;19	1.26	NS
Diaphanosoma	13.9 (11.6)	7.6 (10.3)	3.4 (4.7)	2;19	2.42	NS
Holopedium	27.3 (13.5)	29.5 (17.7)	21.6 (14.7)	2;19	0.66	NS

TABLE 2. (*Concluded*)

Parameter	Allopatric brook charr	Brook charr creek chub	Brook charr white sucker	df	*F*	P
		Zooplankton abundance (no. of individuals/m^3)				
Small cladocerans (<0.6 mm)	61.1 a	187.1 b	306.4 b	2;19	3.96	<0.05
	(24.7)	(145.0)	(364.2)			
Intermediate cladocerans (0.6–1.1 mm)	224.3	283.3	470.6	2;19	2.05	NS
	(136.8)	(241.2)	(315.0)			
Large cladocerans (>1.1 mm)	201.5 ab	170.4 a	350.0 b	2;19	3.80	<0.05
	(157.9)	(149.3)	(146.0)			
Bosmina	8.6 a	101.1 b	208.6 b	2;19	7.19	<0.01
	(4.8)	(148.2)	(267.5)			
Daphnia	292.4	325.1	666.9	2;19	2.84	NS
	(249.6)	(365.1)	(414.8)			
Diaphanosoma	52.8	31.7	50.6	2;19	0.94	NS
	(37.1)	(42.1)	(84.0)			
Holopedium	130.6	179.9	194.1	2;19	0.18	NS
	(81.5)	(132.1)	(113.1)			
		Size (mm) of the different taxa				
Bosmina	0.45 a	0.36 b	0.36 b	2;18	5.19	<0.01
	(0.07)	(0.07)	(0.05)			
Daphnia	0.94	0.94	1.01	2;19	0.48	NS
	(0.08)	(0.23)	(0.13)			
Diaphanosoma	0.79	0.61	0.82	2;13	1.39	NS
	(0.24)	(0.13)	(0.21)			
Holopedium	1.38 a	0.98 b	1.13 b	2;18	11.58	<0.001
	(0.19)	(0.17)	(0.12)			

TABLE 3. Mean percent weight of zooplankton, zoobenthos, and other organisms found in the stomach contents of allopatric and sympatric brook charr populations.

Lake	No. of fish	Mean length (± 1 SD) (mm)	Mean % weight			Mean total stomach content weight (± 1 SD) (g)
			Zooplankton	Zoobenthos	Other prey[a]	
Allopatric						
Bondi	8	211 (36)	77.9	18.9	3.2	0.280 (0.278)
Cerne	8	201 (29)	32.7	59.8	7.5	0.271 (0.222)
Charme	10	218 (31)	41.1	48.9	10.0	0.395 (0.446)
Leonard	13	320 (83)	62.9	24.6	4.8	0.693 (0.509)
Osborn	12	269 (72)	31.7	51.9	16.4	0.514 (0.269)
Simpson	15	207 (24)	56.5	43.2	0.3	0.619 (0.489)
Vautour	15	198 (33)	16.8	83.2	0	0.992 (1.1.15)
Creek chub						
Bourgeois	4	220 (17)	75.0	25.0	0	0.160 (0.136)
Daniet	10	200 (24)	51.1	32.4	16.6	0.551 (0.336)
Petit Carufel	10	163 (36)	2.7	77.3	20.0	0.229 (0.130)
Rose	5	264 (45)	20.9	59.9	19.2	0.204 (0.184)
Tête	15	237 (45)	57.9	27.7	14.4	0.337 (0.298)
Vertnez	10	184 (27)	61.8	30.0	8.2	0.097 (0.089)
White sucker						
Grignon	15	341 (53)	85.3	11.4	3.4	0.728 (1.040)
Jimmy	5	225 (18)	75.0	0	25.0	0.339 (0.577)
Joie	15	208 (44)	56.1	28.3	9.0	0.561 (0.613)
Sauterelle	15	252 (60)	62.3	36.3	1.4	0.954 (0.805)
Vert	12	247 (46)	88.8	2.8	8.3	0.280 (0.222)

[a] Fish and terrestrial insects.

Fishing Data

The mean brook charr yield of the allopatric lakes was significantly higher than those of creek chub and white sucker lakes (Table 2), suggesting that introduced species have an impact on the production of brook charr. The presence of white sucker reduced by almost half the yield of brook charr and the presence of creek chub had a smaller effect.

Feeding Habits of Brook Charr

There was no significant difference in the mean percent weight of zooplankton found in the stomach contents of sympatric and allopatric brook charr populations (Tables 2 and 3). In contrast, brook charr living with white sucker fed significantly less on benthic organisms than the other brook charr populations (allopatric and those living with creek chub) (Tables 2 and 3).

Of the brook charr populations that fed mainly on a prey type (i.e. >50% in mean percent weight), three of the seven allopatric populations (i.e. 43%) fed mainly on zooplankton compared with four of the six populations that live with creek chub (i.e. 67%) and all populations that live with white sucker (i.e. 100%) (Table 3). These tendencies in the data suggest that brook charr shifted their food habits from benthic organisms to zooplankton in the presence of creek chub and (or) white sucker, and they therefore support the conclusions of previous studies done on fewer lakes (Magnan and FitzGerald 1982; S. Tremblay and P. Magnan, in prep.). The results also suggest that the impact of white sucker was stronger than that of creek chub. Although not quantified here, zooplankters found in the stomach contents of charr were mainly *Daphnia* and *Holopedium* (P. Magnan, pers. obs.). For all brook charr populations studied, there was no significant correlation between the mean size of the fish and the food habit data (i.e. mean percent weight of zooplankton, of zoobenthos, and stomach content weight).

Gill Raker Structure of Brook Charr

There was no clear relationship between the number of gill rakers of brook charr and the presence or absence of introduced species (Table 4). However, with only one exception (Lake Petit), there was a significant increase in the length of the longest gill raker of brook charr in the presence of creek chub and (or) white sucker. Also, the ranking of the communities in Table 4 suggests that this increase was greater in the presence of white sucker than in the presence of creek chub.

Zooplankton Community Structure

More than 99% of the 15 475 cladocerans collected in the 22 studied lakes were of four genera: *Bosmina* (13.7%), *Daphnia* (56.4%), *Diaphanosoma* (6.1%), and *Holopedium* (23.3%) (Table 5). In contrast, Chydoridae, *Leptodora*, *Poly-*

TABLE 4. Number of gill rakers and length of the longest gill raker of brook charr in allopatric, creek chub, and white sucker lakes.

Lake	Community	No. of observations	Adjusted mean[a]
	No. of gill rakers ($F = 13.80$, $p < 0.001$)		
Chute noire	Allopatric	10	10.872
Daniet	Creek chub	11	11.164
French	Creek chub	18	11.206
Tête	Creek chub	23	11.211
Cerne	Allopatric	21	11.237
Joie	White sucker	42	11.448
Vautour	Allopatric	71	11.465
Petit Carufel	Creek chub	12	11.532
Sauterelle	White sucker	50	11.696
Petit	Allopatric	42	11.705
Sans-nom	White sucker	18	11.869
Charme	Allopatric	17	11.966
Vert	White sucker	47	12.835
	Length of longest gill raker (mm) ($F = 7.29$, $p < 0.001$)		
Cerne	Allopatric	20	1.596
Chute noire	Allopatric	10	1.755
Charme	Allopatric	17	1.814
Vautour	Allopatric	70	1.821
French	Creek chub	18	1.880
Tête	Creek chub	23	1.930
Petit Carufel	Creek chub	12	1.971
Daniet	Creek chub	11	2.025
Sans-nom	White sucker	18	2.026
Petit	Allopatric	41	2.120
Sauterelle	White sucker	50	2.159
Vert	White sucker	47	2.181
Joie	White sucker	42	2.352

[a] Adjusted means joined by vertical lines are not significantly different as determined by an ANCOVA (fish length as covariable) followed by a Gabriel approximate comparison interval (Sokal and Rohlf 1981). Actual data are presented but analyses were performed on transformed data.

TABLE 5. Composition of the cladoceran communities in the allopatric, creek chub, and white sucker lakes.

	% of total no. of cladocerans					
Lake	*Bosmina*	*Diaphanosoma*	*Daphnia*	*Holopedium*	Others[a]	Total no./m^3
Allopatric						
Bondi	1.8	9.4	84.4	3.8	0.6	3 273
Cerne	0	12.0	72.2	15.7	0.2	4 795
Charme	2.2	24.2	34.4	39.2	0	4 342
Diablos	1.1	2.5	73.6	22.3	0.4	11 418
Leonard	3.7	6.7	48.4	38.7	2.5	4 178
Osborn	1.9	0	57.3	40.9	0	3 765
Simpson	4.8	31.4	42.0	21.8	0	1 993
Vautour	1.8	25.0	37.1	35.8	0.3	3 736
Mean (± 1 SD)	2.2	13.9	56.2	27.3	0.5	4 688
	(1.5)	(11.6)	(18.7)	(13.5)	(0.8)	(2 846)
Creek chub						
Bourgeois	1.2	0	85.1	13.7	0	12 121
Daniet	2.9	0.1	50.0	46.0	1.0	9 011
Grosse	6.9	20.1	18.9	54.1	0	3 062
Petit Carufel	38.5	2.4	16.7	42.0	0.3	5 979
Rose	79.0	5.8	1.9	12.7	0.6	4 631
Tête	1.2	0.5	71.8	25.2	1.2	3 967
Vertnez	4.4	24.4	58.4	12.4	0.4	4 419
Mean (± 1 SD)	19.2	7.6	43.3	29.5	0.5	6 170
	(29.5)	(10.3)	(31.2)	(17.7)	(0.5)	(3 252)
White sucker						
Brise	32.2	0.9	51.8	14.9	0.1	20 218
Grignon	16.4	0	44.5	38.7	0.4	4 756
Jimmy	2.6	10.0	86.9	0	0.5	7 923
Joie	17.5	0	56.0	25.2	1.4	7 115
Jones	21.9	10.0	59.4	8.0	0.7	22 028
Sauterelle	3.6	0	70.6	25.8	0	5 343
Vert	3.5	2.6	54.0	38.5	1.5	8 559
Mean (± 1 SD)	14.0	3.4	60.5	21.6	0.7	10 849
	(11.3)	(4.7)	(14.1)	(14.7)	(0.6)	(7 164)

[a] *Leptodora, Polyphemus*, Chydoridae, and unidentifiable cladocerans.

phemus, and some unidentifiable cladocerans represented only 0.5% of the total sample.

The zooplankton composition was similar among the three groups of lakes (allopatric, creek chub, and white sucker) (Tables 2 and 5). However, in terms of size classes, there was a significantly lower proportion of large zooplankton organisms (>1.1 mm) in creek chub lakes than in allopatric and white sucker lakes (Table 2; Fig. 1).

Zooplankton Abundance

The abundance of *Bosmina* was significantly higher in creek chub and white sucker lakes than in allopatric lakes (Tables 2 and 5). In terms of size classes, the abundance of small crustacean zooplankters (<0.6 mm) was also significantly higher in the creek chub and white sucker lakes than in the allopatric lakes (Table 2; Fig. 1). Also, the number of large (>1.1 mm) zooplankters was significantly higher in the white sucker lakes than in the allopatric and creek chub lakes (Table 2; Fig. 1).

Size Frequency Distribution of the Different Taxa

The mean sizes of *Bosmina* and *Holopedium* were significantly lower in the creek chub and white sucker lakes than in allopatric lakes (Table 2; Fig. 2). It appeared that larger *Holopedium* were replaced by smaller ones in these lakes because, despite the fact that their mean length was reduced, there were no significant differences in their abundance among the different fish communities.

Simple Linear Correlation

The Pearson product-moment correlation analyses revealed that variations in the characteristics of the lakes (e.g. conductivity) could not explain the response variables (Table 6).

General Discussion

The results presented in this paper suggest that creek chub and white sucker had a competitive impact on the brook charr populations. The production of brook charr, in terms of mean annual yield, was significantly lower in the presence of creek chub and white sucker, and the charr shifted their food habits from benthic invertebrates to zooplankton in the presence of introduced species. Such observation in simple fish communities indicates strong interactions between species (Werner 1986). Furthermore, the length of the longest gill raker, and presumably of the other gill rakers, was significantly higher in lakes containing chubs and suckers. As the length of the gill

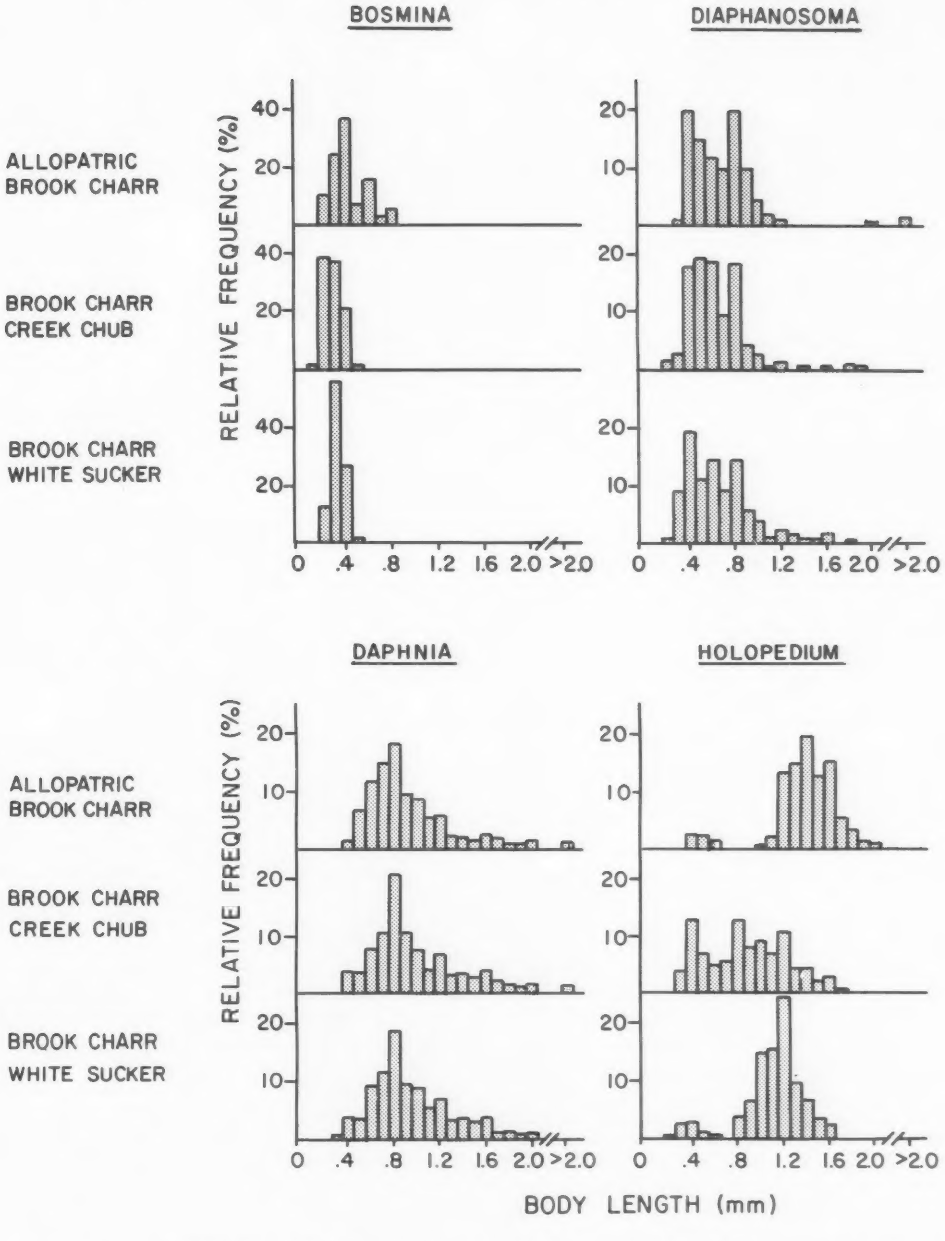

FIG. 2. Size frequency distribution of the four principal taxa found in the 22 studied lakes. Mean number of organisms/m^3 and statistical tests for significant differences among fish communities are given in Table 2.

rakers has been reported to be correlated with the extent of plankton feeding (Lindsey 1981), this latter result was interpreted as a morphological change associated with increased exploitation of zooplankton in sympatry.

The results presented here also suggest that the competitive impact of white sucker was stronger than that of creek chub; changes in food habits, mean yield, and gill raker length were always more pronounced in the presence of the former species. In the same way, changes in the gill raker length of charr appeared to be related to the proportion of zooplankton in their feeding habits and, in the context of this study, to the intensity of competition.

Such changes in the gill raker characteristics might be due to natural selection (genotypic), environmental effect (phenotypic), founder effect, introgression, or by different combinations of these factors (Lindsey 1981; Crowder 1984). Because

TABLE 6. Pearson product-moment correlations between lake characteristics and response variables. Values are correlation coefficients (number of cases in parentheses). *Indicates correlation at $p < 0.05$; only those with $p < 0.01$ were considered significant (see text).

	Brook charr yield	Small cladocerans (<0.6 mm)	Intermediate cladocerans (0.6–1.1 mm)	Large cladocerans (>1.1 mm)
Zooplankton community structure data				
Surface area	−0.251 (26)	−0.105 (22)	0.065 (22)	0.109 (22)
Mean depth	−0.255 (26)	−0.060 (22)	−0.064 (22)	0.172 (22)
Conductivity	−0.142 (26)	0.275 (22)	−0.195 (22)	−0.295 (22)
Modified Ryder's index	0.175 (26)	0.128 (22)	0.012 (22)	−0.241 (22)
Secchi disk transparency	−0.080 (26)	−0.123 (22)	−0.257 (22)	0.465* (22)
Zooplankton abundance data				
Surface area	−0.251 (26)	0.066 (22)	0.228 (22)	0.258 (22)
Mean depth	−0.255 (26)	−0.110 (22)	−0.116 (22)	0.006 (22)
Conductivity	−0.142 (26)	0.065 (22)	−0.237 (22)	−0.304 (22)
Modified Ryder's index	0.175 (26)	0.129 (22)	0.061 (22)	−0.077 (22)
Secchi disk transparency	−0.080 (26)	−0.006 (22)	−0.008 (22)	0.320 (22)

brook charr is not known to naturally interbreed with closely related species (Scott and Crossman 1973) and because related species were not found in the study system the possibility of introgression was not considered here. Also, it is unlikely that the founder effect may have contributed to the observed shift in the gill raker length of the sympatric brook charr. I compared several charr populations, and within each community, the results always varied in the same direction (i.e. gill raker length of charr in the white sucker lakes greater than in creek chub lakes greater than in allopatric lakes, with only one exception). A hypothetical founder effect in one or more communities should have produced random variation in the gill raker length of brook charr populations. Natural selection and environmental effects are the other mechanisms that could explain the shift in gill raker length of sympatric brook charr. There are different kinds of evidence that changes in the gill raker characteristics may be genotypic and (or) phenotypic in Coregonidae, but it is difficult to separate the respective contributions of these two mechanisms (Lindsey 1981; Todd et al. 1981; Crowder 1984). Although it is not necessarily only under genotypic control, gill raker number appears to be less subjected to drastic phenotypic modifications than other morphological characters (e.g. gill raker length; Lindsey 1981). There are examples where gill raker length changed significantly over a short period of time without any change in gill raker number (Loch 1974; Kliewer 1970; this study). In contrast, changes of two or more in gill raker number occur over longer periods of time and are generally attributed to artificial or natural selection (see Lindsey 1981; Crowder 1984). A working hypothesis could be that gill raker length is the first character to respond (phenotypically) to changes in the feeding habits of fish, while gill raker number might change over longer periods, through natural selection.

The niche shift of sympatric brook charr had an impact on zooplankton communities in the creek chub lakes. There was a significantly lower proportion of large zooplankton organisms in these lakes, and the mean length of *Holopedium*, the largest cladoceran, was significantly reduced compared with allopatric lakes. The results also indicated that large zooplankton organisms were replaced by smaller ones in the creek chub lakes. The observation of such an effect on zooplankton communities provides evidence of resource limitation in lake fish communities (Werner 1986). A similar impact on zooplankton community structure was not so clear in the white sucker lakes. The number of small but also of large zooplankton organisms was significantly higher in these lakes when compared with allopatric lakes. Nevertheless, the proportion of zooplankton found in the charr stomachs was much greater in the white sucker lakes than in the two other communities. However, based on the yield data, the size of brook charr populations might be reduced in the white sucker lakes to the point that they had little or no effect on the zooplankton community structure. The only effect that could be seen was a significant decrease in the mean length of *Holopedium* compared with allopatric populations. Results obtained from Sauterelle Lake, a white sucker lake, indicated that the mean length (± 1 SD) of cladocerans eaten by the charrs (mainly *Holopedium* and *Daphnia*) was 1.64 (0.46), 1.55 (0.37), and 1.73 (0.41) mm on June 20, July 12, and August 9, 1985, respectively (S. Tremblay and P. Magnan, in prep.). Thus it seemed that the brook charr ate principally the larger cladocerans (~1.5 mm) in the white sucker lakes and that these larger organisms were replaced by smaller ones in the three size classes studied.

The significant decrease in mean length of *Holopedium* in creek chub and in white sucker lakes suggested that this prey was the first to be selected by the charr when feeding on zooplankton, even if a proportion of the *Daphnia* population overlapped in size with the *Holopedium* population. This could be explained by the fact that *Holopedium* were approximately 1.2 times higher than longer and thus their effective size was higher than that measured in this study.

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Underwater Spectral Attenuation and Its Effect on the Maximum Depth of Angiosperm Colonization[1]

P. A. Chambers and E. E. Prepas

Department of Zoology, University of Alberta, Edmonton, Alta. T6G 2E9

Chambers, P. A., and E. E. Prepas. 1988. Underwater spectral attenuation and its effect on the maximum depth of angiosperm colonization. Can. J. Fish Aquat. Sci. 45: 1010–1017.

Data collected from 23 Alberta lakes and literature values for 45 other north temperate lakes were used to develop regression models to evaluate the effect of underwater light quality on the maximum depth of angiosperm colonization. Unlike most north temperate lakes, eutrophic Alberta lakes have unusually low levels of dissolved colour and, as a result, transmit blue light particularly well. Comparison of regression equations relating the maximum depth of angiosperm colonization (z_c) and Secchi depth (D) for lakes with low colour ($z_c^{0.5} = 0.69 \log(D) + 1.76$) and with high colour ($z_c^{0.5} = 1.22 \log(D) + 1.10$) showed that for any Secchi depth, aquatic angiosperms colonized to greater depths in lakes with low colour. These results demonstrate that light quality as well as light quantity determine the maximum depth of angiosperm colonization in lakes. Regional differences in the relation between z_c and Secchi depth may therefore be due to variations in the underwater light spectrum.

On utilise des données recueillies dans 23 lacs de l'Alberta et des données publiées sur 45 autres lacs tempérés du nord pour élaborer des modèles de régression destinés à l'évaluation de l'incidence de la qualité de la lumière sous l'eau sur la profondeur maximum de la colonisation par les angiospermes. Au contraire de la plupart des lacs tempérés du nord, les lacs eutrophes de l'Alberta montrent des niveaux exceptionnellement faibles de matières colorées et transmettent donc particulièrement bien la lumière bleue. Une comparaison des équations de régression établissant une relation entre la profondeur maximum de la colonisation par les angiospermes (z_c) et la profondeur de Secchi (D) dans les lacs à faible niveau de matières colorées ($z_c^{0,5} = 0{,}69 \log(D) + 1{,}76$) et à niveau élevé de matières colorées ($z_c^{0,5} = 1{,}22 \log(D) + 1{,}10$) révèle qu'à n'importe quelle profondeur de Secchi, les angiospermes aquatiques se sont établis à de plus grandes profondeurs dans les lacs à faible niveau de matières colorées. Ces résultats révèlent que la qualité de la lumière ainsi que la quantité déterminent la profondeur maximum de la colonisation lacustre par les angiospermes. Les différences régionales de la relation entre z_c et la profondeur de Secchi peuvent donc être le résultat de variations du spectre lumineux subaquatique.

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Models have recently been developed to predict the maximum depth of aquatic macrophyte colonization from Secchi disc transparency (Canfield et al. 1985; Chambers and Kalff 1985). These models show that the maximum depth of angiosperm colonization is positively correlated with underwater light penetration in a wide variety of lake types, as well as for temporal changes within a lake. Except in a few oligotrophic lakes where the euphotic zone extends below the thermocline and temperature limits plant depth distribution (Dale 1986), underwater light is now generally regarded as the prime determinant of the maximum depth to which aquatic angiosperms can grow.

However, while Secchi depth is a good predictor of the maximum depth of macrophyte colonization, it does not discriminate between the effects of phytoplankton and dissolved colour on underwater light penetration. The use of Secchi disc transparency as a measure of trophic conditions is based on the assumption that the transparency of lake water is controlled by algal turbidity (e.g. Carlson 1977). Yet, water colour has been shown to exert a significant effect on Secchi depth (Brezonik 1978; Canfield and Hodgson 1983). Thus, lakes with similar Secchi depths may differ considerably in spectral energy distribution.

We hypothesize that light quality (colour) as well as light quantity (irradiance) control the maximum depth of angiosperm colonization and that consideration of both attributes of the underwater light climate will explain scatter and regional differences in the published models. Data on both water colour and aquatic macrophyte depth distribution are relatively scarce, however, and thus we used underwater spectral attenuation as an indicator of water colour. To test the hypothesis that both irradiance and water colour determine aquatic angiosperm depth distribution, data collected from 23 Alberta lakes along with literature values for 45 other north temperate lakes were used to develop regression models relating the maximum depth of angiosperm colonization and Secchi depth for two sets of lakes with distinctly different spectra.

Materials and Methods

Secchi disc transparency, the maximum depth of angiosperm colonization, and chlorohyll *a* (Chl *a*) concentration were measured in 23 Alberta lakes in late July or August (the period of peak macrophyte abundance). In each lake, the maximum depth of aquatic angiosperm colonization was determined by SCUBA or skin divers who swam from shore to the depth where aquatic angiosperms were no longer observed. Integrated water samples were collected from the euphotic zone with weighted Tygon tubing, placed in opaque bottles which were completely filled and filtered under low pressure (-50 kPa) through Whatman GF/C filters within 10 h of collection. The filters were placed in petri dishes, wrapped in aluminum foil, frozen, and analyzed within 2 wk. Chl *a* was determined in triplicate with a spectrophotometric technique based upon the ethanol extraction procedure of Ostrofsky (unpublished) as described by Bergmann and Peters (1980) or a fluorometric procedure and acetone extraction (Yentsch and Menzel (1963) as modified by Holm-Hansen et al. (1965)). (Previous comparisons of Chl *a* values from duplicate sets of samples have shown that results of the two methods do not differ significantly (Prepas and Trew 1983)). The lakes were then classified on the basis of Chl *a* as oligotrophic (Chl $a < 2\ \mu g \cdot L^{-1}$), mesotrophic (Chl $a > 2$ and $< 12\ \mu g \cdot L^{-1}$), or eutrophic (Chl $a > 12\ \mu g \cdot L^{-1}$).

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[1] A contribution to the Narrow Lake Project, Meanook Biological Research Station.

In 12 representative lakes, underwater spectral irradiance was measured with a Techtum Instrument QSM-2500 quanta spectrometer which scans between 400 and 740 nm by means of a continuous wedge interference filter. The instrument was lowered at 0.25- or 0.5-m intervals from 0.5 m below the water surface to within 0.5 m of the sediments or a maximum of 10 m, providing light was still detected. Vertical diffuse attenuation coefficients (ln units per metre) were calculated by linear regression for PAR (400–700 nm) and for each 20-nm waveband (from 400 to 740 nm), measured by planimetry with a Placom Digital Planimeter model KP-90 (Koizumi Sokki Manufacturing Co., Ltd). Colour was determined with the platinum–cobalt method on a Hellige-Aqua Tester (model 611-A) for integrated water samples collected from the euphotic zone at the site of the spectral measurements.

For an additional 45 north temperate lakes, data on Secchi depth, colour, maximum depth of angiosperm colonization, and underwater light quality were obtained from the literature. Since most of these underwater light quality data were obtained with a photocell with interchangeable glass broad-band-pass filters (i.e. Chance filters: OR with $\lambda_{\max}$ of 680 nm, OG with $\lambda_{\max}$ of 550 nm, and OB with $\lambda_{\max}$ of 450 nm; or Schott filters: RG with $\lambda_{\max}$ of 630 nm, VG$_9$ with $\lambda_{\max}$ of 525 nm, and BG$_{12}$ with $\lambda_{\max}$ of 460 nm), the results were expressed in terms of red, green, or blue light, usually as vertical diffuse attenuation coefficients (K). However, for data presented as absolute or percent surface values of red, green, or blue light plotted at depth or as the depth to which 1% red, green, or blue light penetrated, attenuation coefficients for each waveband were calculated from the Beer–Lambert equation. K_{PAR} was calculated as the mean of the attenuation coefficients for blue, green, and red light (Vollenweider 1974), unless otherwise given by the investigators. For the Alberta data, as well as others collected with a scanning spectrophotometer, the wavelengths 660–680, 540–560, 440–460, and 400–700 nm were taken to represent red, green, and blue light and PAR, respectively.

Data on Secchi depth and maximum depth of angiosperm colonization for the 23 Alberta lakes and the 45 other north temperate lakes were combined and regression equations relating maximum depth of colonization to Secchi depth were developed for low- and high-colour lakes. Because data on water colour were relatively scarce, low- and high-colour lakes were distinguished on the basis of underwater light quality. Since dissolved organic material, the prime determinant of water colour, absorbs strongly in the blue and ultraviolet regions of the spectrum (Hall and Lee 1974), we used the ratio of the attenuation coefficients of blue and red light (K_B/K_R) as the distinguishing criterion and defined low-colour lakes as those with K_B/K_R less than 1.3 and highly coloured lakes as having K_B/K_R ratios greater than 1.3. This distinction generally corresponds to a water colour of about 30–50 mg $\mathrm{Pt} \cdot \mathrm{L}^{-1}$.

Statistical analyses were performed using STATGRAPHICS statistical software (Statistical Graphics Corporation, 1985) on an APCO-XT microcomputer. Data for the maximum depth of angiosperm colonization – Secchi depth model were transformed (square-root and logarithmic transformations to the y- and x-axes, respectively) to allow direct comparison with the model of Chambers and Kalff (1985). The percent PAR reaching the maximum depth of angiosperm colonization was calculated from the Beer–Lambert equation. For Alberta lakes without irradiance data, PAR attenuation coefficients (K_{PAR}) were estimated from Secchi depth (D) assuming $K_{\mathrm{PAR}} = 2.15/D$ (P.A. Chambers and E. E. Prepas, unpubl. data).

Results

Description of Alberta Lakes

The 23 study lakes are spread over a large area (1.38×10^5 km^2) in central Alberta (52°27′ to 54°45′ N, 110°05′ to 118°04′ W) in the drainage basins of four major river systems (Athabasca, North Saskatchewan, Battle, and Beaver) (Table 1). All but three lakes are located in the boreal mixedwood and aspen parkland regions of Alberta (Strong and Leggat 1981) and are underlain by Upper Cretaceous bedrock covered by glacial till 10–200 m thick. Climate is continental; mean annual precipitation is 300–550 mm and mean annual lake evaporation is 450–700 mm (Fisheries and Environment Canada 1978). Three mountain lakes (Cavell, Maligne, and Gregg) are located in the alpine, subalpine, and boreal foothill regions of Alberta, respectively (Strong and Leggat 1981). The basins of these lakes are formed primarily from Devonian and Carboniferous limestone and dolomite. The lakes are fed to varying degrees by glacial meltwater: Cavell Lake and, to a lesser extent, Maligne Lake are fed directly by glaciers throughout the summer whereas Gregg Lake receives glacial meltwater only during spring runoff.

The 12 lakes where underwater spectral irradiance was measured are representative of the geographic, morphometric (volume, surface area, mean, and maximum depths), and trophic (Chl *a*) extremes of the original 23 lakes (Table 1). The three mountain lakes (Cavell, Maligne, and Gregg) and Cold Lake are oligotrophic, Narrow, Ethel, and Long are mesotrophic, and Baptiste, Upper Mann, Tucker, Joseph, and Cooking lakes are eutrophic. Comparison of Secchi depths measured at the same time as spectral irradiance and mean values for the open-water period over several years showed that underwater light conditions prevailing at the time of spectral irradiance measurements were representative of most summers (E. E. Prepas and Alberta Environment, Planning Division and Water Quality Control Branch, unpubl. data).

Underwater Light Climate

In oligotrophic Alberta lakes, spectral attenuation coefficients were usually less than 1.0 and maximum transmittance

TABLE 1. Background data for 23 Alberta lakes in which the maximum depth of aquatic angiosperm colonization was measured: location, surface area (Area), volume (V), maximum depth (z), mean depth ($\bar{z}$), chlorophyll a (Chl a) concentration, colour, and Secchi depth (D) measured in late July or August. Asterisks indicate lakes in which underwater spectral irradiance was measured; dashes indicate data not available. Unless otherwise referenced, morphometric data were obtained from Alberta Environment and all other data were collected in this study.

Lake	Coordinates N	Coordinates W	Area (km²)	V ($\times 10^6$ m³)	z (m)	$\bar{z}$ (m)	Chl a (μg·L⁻¹)	Colour (mg Pt·L⁻¹)	D
Baptiste*	54°45′	113°33′	9.2	86	27.5	9.3	12	30	1.5
Buffalo–2° basin	52°30′	112°52′	82.7	235	2.8	6.5	12[a]	—	1.8[a]
–Main basin	52°27′	112°58′					9[a]	—	0.8[a]
Cavell*	52°42′	118°04′	0.02[c]	—	6.2[c]	—	0.9	5	1.4
Coal	53°05′	113°16′	10.4	36.3	5.5	3.5	76[a]	—	0.3[a]
Cold*	54°33′	110°05′	373.0[e]	19 878[e]	100.6[e]	53.3	1.5	5	6.7
Cooking*	53°26′	113°02′	44.3	106	4.1	2.4	123	48	0.2
Crimson	52°27′	115°02′	2.43	5.35	9.0	2.2	3.2[b]	—	3.5[b]
Driedmeat	52°52′	112°45′	9.1	16.4	3.6	1.8	128[a]	—	0.8[a]
Ethel*	54°32′	110°21′	4.8	32	33	6.6	2.5	10	4.0
Garner	54°12′	111°14′	7.1	50.63	15	7.1	4.1[b]	—	3.6[b]
Gregg*	53°31′	117°48′	1.4	—	—	—	0.8	7.5	6.1
Joseph*	53°17′	113°04′	6.7	26	3.4	2.4	66	50	0.2
Long*									
N basin	54°36′	113°39′	1.6[f]	15[f]	28	9.4[f]	3.9	20	3.3
S basin	54°35′	113°40′					3.6	16	4.2
Maligne*	52°40′	117°31′	21.8[g]	883[g]	96[g]	40.5	0.5	2.5	5.2
Muriel	54°09′	110°41′	63.27	449	11.4	6.6	6.1[b]	—	2.8[b]
Nakamun	53°53′	114°12′	3.16[h]	15.77[h]	8.0[h]	4.5	18.7[b]	—	1.0[b]
Narrow*	54°35′	113°37′	1.1[f]	16[f]	36	14.4[f]	2.1	7.5	5.5
Pigeon	53°01′	113°59′	94.8	598	10.2	6.3	14[b]	—	1.5[b]
Sandy									
N basin	53°48′	114°03′	11.24	14.8	4.6	1.5	44[b]	—	0.7[b]
S basin	53°47′	114°02′					22[b]	—	1.2[b]
Skeleton	54°37′	112°43′	8.78	57.8	17	6.6	27[h]	—	1.3[b]
Tucker*	54°32′	110°37′	7.2	21	6.5	2.9	36	10	0.65
Upper Mann*	54°09′	111°30′	4.6	27	10	5.9	16	10	1.05
Wizard	53°07′	113°55′	2.4[d]	14.8[d]	11.3[d]	6.2	26[b]	—	0.9[b]

[a] Alberta Environment, Planning Division.
[b] Alberta Environment, Water Quality Control Branch.
[c] Anderson (1974).
[d] Babin (1984).
[e] Paetz and Zelt (1974).
[f] Prepas and Trimbee (1987).
[g] Rawson (1942).
[h] Riley and Prepas (1984).

(i.e. minimum attenuation) was in the green region (520–580 nm) (Fig. 1). The clearest lakes, Cold and Maligne, showed peak attenuation in the far red region (700–740 nm); in Gregg and Cavell lakes, attenuation increased in both the blue and far red wavebands. The mesotrophic lakes exhibited similar spectral distributions: attenuation was lowest in the green wavebands and highest in the blue or far red regions of the spectrum. In contrast, the eutrophic Alberta lakes showed very different spectral distributions. Attenuation coefficients were generally greater than 1.0 and maximum transmittance was in the blue region (400–440 nm) for all but the clearest (Upper Mann) lake. The two lakes with Chl a concentrations greater than 60 $\mu g \cdot L^{-1}$ (Joseph and Cooking) also showed broad bands (500–740 nm) of high attenuation (2.5–4.8 ln units·m⁻¹), while peak attenuation for lakes with Chl a concentrations between 12 and 35 $\mu g \cdot L^{-1}$ was 1.3–2.3 ln units·m⁻¹.

Spectral attenuation coefficients for other (i.e. non-Albertan) north temperate lakes are shown in Table 2. In 18 of the 24 oligotrophic lakes, green was the most penetrating waveband; far red was usually least transmitted. The mesotrophic lakes also showed peak transmittance in the green waveband; however, here, blue was the most attenuated waveband in 13 of the 15 lakes. The eutrophic lakes all showed peak attenuation in the blue region of the spectrum; maximum transmittance was in the green or red wavebands.

Comparison of spectral energy distributions between Alberta and other north temperate lakes showed different patterns in underwater light quality with increasing trophy (Table 3). In Alberta lakes, increasing trophy is associated with a shift in maximum transmittance from the green to the blue waveband. In contrast, in other north temperate lakes, blue light was rapidly attenuated and there was increased penetration of red light relative to the other wavebands. Comparison of the ratio of the attenuation coefficients of blue and red light also showed that K_B/K_R ratios were significantly lower ($P < 0.05$) in eutrophic lakes in Alberta than in other north temperate areas.

Measurements of spectral attenuation for our 12 Alberta lakes showed that all but one (Gregg) had K_B/K_R values less than 1.3 and therefore represent low-colour lakes. In the case of Gregg Lake, however, its comparatively large effective drainage basin, which is dominated by a coniferous forest, together with unusually high precipitation recorded during the month prior to sam-

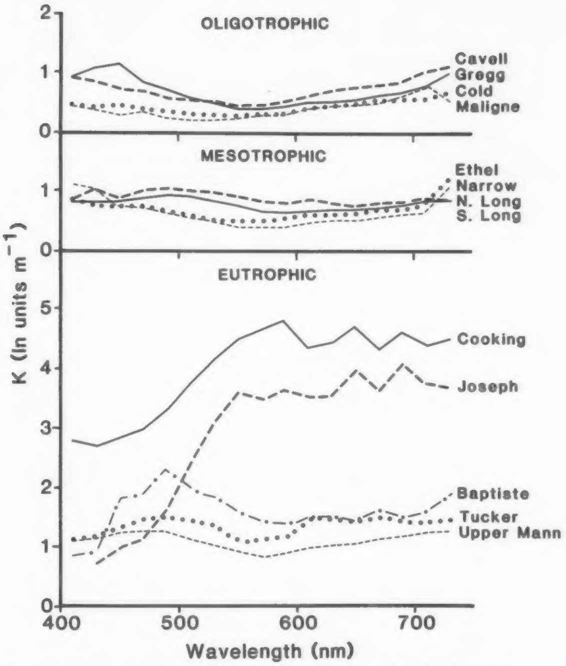

FIG. 1. Vertical diffuse attenuation coefficients as a function of wavelength for 12 Alberta lakes classified as oligotrophic (Chl *a* $< 2\ \mu g \cdot L^{-1}$), mesotrophic (Chl $a > 2$ and $< 12\ \mu g \cdot L^{-1}$), or eutrophic (Chl $a > 12\ \mu g \cdot L^{-1}$).

pling (twice the 30-yr long-term average) may be responsible for its high K_B/K_R ratio. Since the nine lakes located in the Alberta boreal parkland encompass the morphometric and trophic extremes of parkland lakes (Table 1) and all had K_B/K_R ratios less than 1.3, we considered the additional 11 parkland lakes for which we have data on Secchi depth and maximum depth of colonization to have low colour.

Aquatic Angiosperm Depth Distribution

Regression equations were developed relating the maximum depth of angiosperm colonization to Secchi depth for both low- and high-colour lakes (Fig. 2). The alpine and subalpine Alberta lakes, Cavell and Maligne, were omitted from the models because aquatic angiosperms were confined to depths with temperatures greater than 10°C, indicating that temperature rather than irradiance limits distribution (Dale 1986). For lakes with low colour ($n = 44$) the relationship was

$$(z_c)^{0.5} = 0.69 \log(D) + 1.76 \quad r = 0.81, P < 0.0001$$

where z_c represents the maximum depth of angiosperm colonization (metres) and D represents Secchi depth (metres). The regression equation for the highly coloured lakes ($n = 29$) was

$$(z_c)^{0.5} = 1.22 \log(D) + 1.10 \quad r = 0.86, P < 0.0001.$$

Both models encompass a wide range of Secchi depths, from less than 20 cm to greater than 9 m. Comparison of the models for low- and high-colour lakes showed that the regression lines were significantly different (slope (t-test): $t = 5.03$, $P < 0.001$) and intersected at a Secchi depth of about 18 m. Thus, over the entire range of our data, aquatic angiosperms colonized to greater depths, relative to Secchi depth, in lakes with low colour.

Estimates of the percent of surface PAR received at the maximum depth of angiosperm colonization were determined from K_{PAR} for both low- and high-colour lakes (Table 4). In the low-colour lakes, the percent surface PAR at the maximum depth of angiosperm colonization decreased significantly ($P < 0.05$) with increasing trophy. In contrast, increasing trophy in the highly coloured lakes was associated with an increase in percent PAR at the maximum depth of angiosperm colonization.

Discussion

Alberta lakes differ significantly from other north temperate lakes in the relationship between trophic state and underwater light quality (Table 3). With increasing trophy, maximum transmittance in Alberta lakes shifted from the green to the blue waveband. In contrast, other north temperate lakes exhibit increased attenuation of blue light in response to increasing trophy. These differences in underwater light quality in mesotrophic and eutrophic lakes in Alberta and elsewhere are related to water colour. Compared with other geographic areas, Alberta lakes are, on average, less coloured (Table 5). Dissolved organic material (also referred to as gelbstoff, gilvin, yellow substances, humic acid, etc.) is the prime determinant of dissolved water colour and consists of a complex mixture of plant breakdown products that have leached out of the soils of the drainage basin and into the lake (Christman and Ghassemi 1966). As this material shows preferential absorption in the blue and ultraviolet regions of the spectrum (Hall and Lee 1974), increased water colour is associated with increased attenuation of blue light.

The low levels of colour in mesotrophic and eutrophic lakes in Alberta and other prairie provinces (Rawson 1960) are attributable to minimal inputs of dissolved organic matter as a result of limited surface water inflow. In western Canada off the Precambrian Shield and east of the Rocky Mountains, annual lake evaporation exceeds annual precipitation (Fisheries and Environment Canada 1978) and effective drainage areas are small due to low relief. Surface runoff is therefore minimal. Of the 23 Alberta lakes, only six (Cavell, Maligne, Gregg, Cold, Driedmeat, and Tucker) have continuous stream inflow during the summer months, and of these, three are mountain lakes in areas of high relief. A survey of 530 Wisconsin lakes likewise demonstrated that lakes with little or no colour (<10 mg $Pt \cdot L^{-1}$) were almost always seepage lakes with no stream inflow whereas highly coloured lakes (>70 mg $Pt \cdot L^{-1}$) were usually drainage lakes (Juday and Birge 1933).

The observation that low water colour is characteristic of productive prairie lakes and is due to low surface runoff is consistent with results from studies of phosphorus loading to these lakes (Riley and Prepas 1984). Unlike lakes on the Precambrian Shield, where external loading is the major phosphorus source and a good predictor of lake trophic status (Dillon and Rigler 1975), the productivity of shallow eutrophic lakes in western Canada is strongly influenced by internal phosphorus loading (Riley and Prepas 1984). In these lakes, terrestrial phosphorus loading usually occurs for short and unpredictable periods of time.

Alberta lakes also differ from other freshwaters in the relationship between the maximum depth of angiosperm colonization and Secchi depth (Fig. 2). When z_c – Secchi depth relationships were compared for low- and high-colour lakes in the

TABLE 2. Attenuation coefficients for blue (K_B), green (K_G), and red (K_R) light and PAR (K_{PAR}), Secchi disc transparency (D), colour, and the maximum depths of angiosperm colonization (z_c) for 45 north temperate lakes. Lakes were classed according to the trophic status assigned by the investigators. Asterisks indicate low-colour lakes (i.e. $K_B/K_R < 1.3$); dashes indicate data not available.

Lake	Location	K_B	K_G	K_R	K_{PAR}	Colour (mg Pt·L^{-1})	D (m)	z_c (m)	Reference(s)
Oligotrophic									
Awe	Scotland	3.73	1.05	1.59	2.12	28	3.2	2.6	Spence 1964; Bailey-Watts and Duncan 1981
Balnagowan*	Scotland	0.29	0.13	0.43	0.28	—	9.5	6.5	Spence 1982, and pers. comm.
Borralie*	Scotland	0.29	0.16	0.45	0.37	—	7.7	6.0	Spence 1982, and pers. comm.
Croispol*	Scotland	0.29	0.18	0.43	0.63	—	6.9	6.0	Spence et al. 1971a; Spence 1982, and pers. comm.
Crystal*	Wisconsin	0.12	0.08	0.61	0.25	0	10.7	4.0	Fassett 1930; Birge and Juday 1930, 1931
Fievatn	Norway	4.49	2.05	1.44	1.81	—	3.2	2.9	Hauge 1957, after Braarud and Aalen 1938
Fiolen*	Sweden	0.81	0.42	1.27	0.59	11	4.6	4.6	Thunmark 1931; Aberg and Rodhe 1942
George*	New York	0.28	0.23	0.54	0.26	—	6.5	7.0	Sheldon and Boylen 1977; Stross 1979
Grane Langsø*	Denmark	0.33	0.21	0.44	0.35	2.5	10.7	5.0	Nygaard 1958; Nygaard and Sand-Jensen 1981
Kejimkujik	Nova Scotia	3.62	1.39	1.41	1.96	67	1.8	2.0	Beauchamp et al. 1987; Beauchamp (pers. comm.)
Lomond	Scotland	2.08	0.78	0.74	1.20	10	5.5	2.0	Spence 1964; Bailey-Watts and Duncan 1981
Lundarvatn*	Norway	0.39	0.24	0.46	0.26	—	9	4.5	Hauge 1957
Mirror*	New Hampshire	0.54	0.33	0.49	0.34	—	6.4	7.2	Likens 1985
Morar	Scotland	1.36	0.67	0.75	0.93	8	8.0	5.0	Bailey-Watts and Duncan 1981
Naevestadfjord	Norway	1.56	0.83	0.87	1.11	—	3	2.6	Hauge 1957, after Braarud and Aalen 1938
Päärjärvi	Finland	9.21	3.65	1.77	4.88	158	2.3	2.0	Kansanen and Niemi 1974; Eloranta 1978
Pebbleloggitch	Nova Scotia	4.20	1.69	1.52	2.23	93	1.5	1.0	Beauchamp et al. 1987; Beauchamp (pers. comm.)
Saimaa II*	Finland	0.44	0.24	0.56	0.41	6	11.2	5.7	Eloranta and Marja-aho 1982
Shiel	Scotland	2.03	0.75	0.71	1.16	8	6.6	5.0	Bailey-Watts and Duncan 1981
Stechlin*	Germany	0.46	0.29	0.54	0.43	—	7.2	4.0	Casper 1985
Trout*	Wisconsin	0.59	0.31	0.55	0.48	6	3.2	6.5	Birge and Juday 1931; Wilson 1941
Vrana*	Yugoslavia	0.10	0.11	0.46	0.22	5	14.0	7.7	Golubić 1961, 1963
Wastwater*	England	0.18	0.12	0.38	0.23	—	15.0	6.0	Macan 1970; Spence 1982; after Talling 1971
Weber*	Wisconsin	0.24	0.15	0.39	0.28	8	8.0	4.0	Birge and Juday 1930; Fassett 1930
Mesotrophic									
Almind	Denmark	0.97	0.50	0.60	0.54	—	4.6	3.6	Sand-Jensen and Søndergaard 1981
Derwentwater*	England	0.47	0.32	0.42	0.40	—	3.9	5.0	Macan 1970; Spence 1982, after Talling 1971
Esthwaite	England	0.77	0.48	0.52	0.59	—	3.7	3.1	Macan 1970; Spence 1982, after Talling 1971
Hampen	Denmark	0.96	0.54	0.64	0.60	—	3.7	4.2	Sand-Jensen and Søndergaard 1981
Muskellunge*	Wisconsin	0.48	0.34	0.50	0.45	4	3.3	7.0	Birge and Juday 1930; Wilson 1935
Nehmitz*	Germany	0.65	0.55	0.62	0.60	—	6.4	4.5	Casper 1985
Obisary	Scotland	0.58	0.26	0.38	0.41	—	4.7	5.0	Spence et al. 1979, and pers. comm.
Saimaa I	Finland	5.05	2.00	1.26	2.77	55	2.4	2.5	Eloranta and Marja-aho 1982
Saimaa III		2.77	1.10	1.15	1.67	33	4.9	2.7	
Silver*	Wisconsin	0.32	0.24	0.67	0.43	8	3.2	6.0	Birge and Juday 1930, 1931; Wilson 1935
Slaaen*	Denmark	0.58	0.33	0.54	0.51	—	5.2	5.5	Sand-Jensen and Søndergaard 1981
Straken	Sweden	4.08	0.89	1.36	0.81	29	2.9	3.2	Aberg and Rodhe 1942; Hutchinson 1975, after Blomgren and Naumann 1925
Uanagan	Scotland	0.62	0.37	0.43	0.47	—	3.3	3.9	Spence et al. 1971a; Spence 1982, and pers. comm.
Urigill	Scotland	1.95	0.86	0.92	1.24	—	1.4	3.0	Spence and Allen 1979; Spence 1982, and pers. comm.
Vechten*	Netherlands	1.06	0.63	0.93	0.60	—	3.5	5.0	Best 1982; Steenberger and Verdouw 1982
Windermere	England	0.66	0.35	0.58	0.53	—	6.3	4.6	Macan 1970; Spence 1982, after Talling 1971
Eutrophic									
Byrup	Denmark	4.43	2.18	2.38	1.43	—	1.4	0.3	Sand-Jensen and Søndergaard 1981
Canadarago	New York	1.06	0.62	0.74	0.69	—	1.2	2.5	Han et al. 1980
Furesø	Denmark	1.04	0.58	0.74	0.79	—	4.5	6.0	Berg and Røen 1958; Nygaard 1958
Leven	Scotland	2.01	1.07	1.04	2.45	—	1.5	1.0	Bindloss et al. 1972; Jupp et al. 1974
Lyngby Sø[a]	Denmark	—	—	—	—	37	0.3	0.4	Olsen 1955
Lowes	Scotland	0.97	0.59	0.60	0.72	—	2.1	3.9	Spence 1982, and pers. comm.
Saimaa IV	Finland	1.54	0.69	1.12	1.12	10	4.2	2.7	Eloranta and Marja-aho 1982
Trummen (1969)	Sweden	15.35	12.12	10.96	12.81	40	0.2	0.0	Gelin 1976; Gelin and Ripl 1978
Trummen (1973)		3.41	2.71	2.37	2.83	—	0.7	1.0	

[a] Spectral data not available; investigator states the lake is brown in colour.

TABLE 3. Attenuation coefficients for blue, green, and red light and the ratio of the attenuation coefficients for blue and red light ($\bar{x}$ ± SE) for Alberta and other north temperate lakes.

	K_B	K_G	K_R	K_B/K_R
Alberta lakes				
Oligotrophic	0.66 ± 0.19	0.33 ± 0.05	0.62 ± 0.05	1.04 ± 0.26
Mesotrophic	0.81 ± 0.04	0.65 ± 0.12	0.70 ± 0.05	1.16 ± 0.04
Eutrophic	1.64 ± 0.33	2.36 ± 0.70	2.44 ± 0.65	0.81 ± 0.16
North temperate lakes				
Oligotrophic	1.57 ± 0.44	0.67 ± 0.17	0.78 ± 0.09	1.47 ± 0.25
Mesotrophic	1.37 ± 0.35	0.61 ± 0.11	0.72 ± 0.08	1.63 ± 0.22
Eutrophic	3.73 ± 1.72	2.57 ± 1.39	2.49 ± 1.24	1.56 ± 0.08

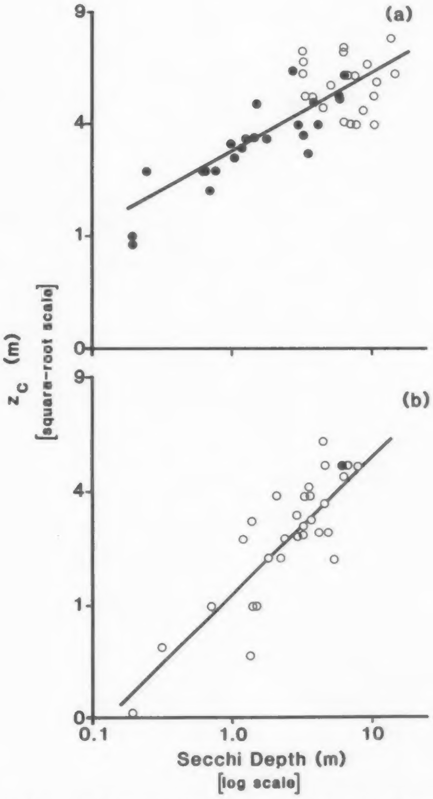

FIG. 2. Relationship between the maximum depth of angiosperm colonization (z_c) and Secchi depth for lakes (a) low in dissolved colour ($K_B/K_R < 1.3$) and (b) high in dissolved colour ($K_B/K_R > 1.3$). Solid symbols represent Alberta lakes; open symbols represent other north temperate lakes.

TABLE 4. Percent of surface PAR ($\bar{x}$ ± SE (n)) received at the maximum depth of angiosperm colonization in low- and high-colour lakes.

	% PAR at z_c	
	Low colour	High colour
Oligotrophic	14.8 ± 2.3 (16)	3.4 ± 1.2 (10)
Mesotrophic	6.2 ± 1.0 (14)	8.4 ± 2.0 (10)
Eutrophic	1.7 ± 0.6 (14)	13.4 ± 7.7 (8)

temperate northern hemisphere, we found that for any Secchi depth, aquatic angiosperms colonized to greater depths in lakes with low levels of dissolved colour. Our model for low-colour lakes included only Alberta data for Secchi depths less than 3.3 m, as a literature search failed to uncover additional north temperate lakes with K_B/K_R values less than 1.3 and Secchi depth less than 3.3 m. This observation is consistent with our conclusion that productive lakes in western Canada off the Precambrian Shield and east of the Rocky Mountains are lower in water colour than those in other north temperate locations. In a study of 90 lakes covering a wide range of lake trophy and water colour, Chambers and Kalff (1985) found that the regression equation relating the maximum depth of angiosperm colonization to Secchi depth was

$$(z_c)^{0.5} = 1.33 \log(D) + 1.40.$$

This regression line is intermediate between our regression lines for low- and high-colour lakes, which is expected because the former includes both clear and brown-water lakes.

Estimates of the percent of surface PAR received at the maximum depth of colonization further confirm that in eutrophic lakes, aquatic angiosperms are found at lower total irradiance in lakes with less colour (Table 4). However, in oligotrophic lakes, the percent PAR at the maximum depth of angiosperm colonization was significantly lower ($P < 0.05$) in highly coloured lakes. This is surprising, since our $z_c - D$ regression lines intersect at a Secchi depth of about 18 m, indicating that even under oligotrophic conditions, aquatic angiosperms are found at greater depths in lakes with low colour. The observation that in highly coloured oligotrophic (i.e. dystrophic) lakes, aquatic angiosperms are restricted to shallower depths and receive less PAR than plants in low-colour oligotrophic lakes appears related to changes in the relation between K_{PAR} and Secchi depth, in that the product of K_{PAR} and Secchi depth was significantly greater ($P < 0.05$) for oligotrophic lakes with high colour (6.19 ± 0.86; $\bar{x}$ ± SE) than with low colour (2.70 ± 0.22).

Our results demonstrate that in Alberta lakes, increasing trophy is associated with an increase in blue light penetration and is due to low levels of dissolved colour caused by minimal surface runoff. In contrast, other north temperate lakes transmit predominately green or red light and have higher levels of dissolved colour. With increasing trophy, aquatic angiosperms in lakes with low colour were also found at greater depths than in coloured lakes with similar Secchi depths (Fig. 2). We suggest that differences in underwater spectral attenuation are responsible for variations in the maximum depth of angiosperm colonization for lakes with similar Secchi depths. While few studies have examined the ecological significance of light quality for freshwater macrophytes, Spence et al. (1971b) and Stross

TABLE 5. Mean values and related statistics for lake colour (mg $Pt \cdot L^{-1}$) in Alberta and other geographic locales.

Region	Mean	SE	Range	Number in sample	Reference
Alberta	25	3.2	3–104	52	E.E. Prepas and P. A. Chambers (unpubl. data)
Ontario (ELA)	32	4.7	5–140	40	Armstrong and Schindler 1971
Wisconsin	46	2.3	0–340	530	Juday and Birge 1933
Nova Scotia	53	9.6	5–140	20	Catling et al. 1986
Finland	68	8.9	5–187	30	Eloranta 1978

(1979) have implicated light quality in the control of maximum depths of colonization in two freshwater angiosperms and the macroalgae *Chara*. We suggest that in freshwater systems water colour as well as irradiance control the maximum depth of angiosperm colonization and that regional differences in the relationship between angiosperm depth distribution and Secchi depth may be due in part to variations in the underwater spectrum.

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Biochemical Genetic Differentiation of Lake Trout (*Salvelinus namaycush*) Stocks of the Great Lakes Region[1]

P. E. Ihssen, J. M. Casselman, and G. W. Martin

Ontario Ministry of Natural Resources, Research Section, Fisheries Branch, Box 50, Maple, Ont. L0J 1E0

and R. B. Phillips

Department of Zoology, University of Wisconsin-Milwaukee, Lapham Hall 577, Box 413, Milwaukee, WI 53201, USA

Ihssen, P. E., J. M. Casselman, G. W. Martin, and R. B. Phillips. 1988. Biochemical genetic differentiation of lake trout (*Salvelinus namaycush*) stocks of the Great Lakes region. Can. J. Fish. Aquat. Sci. 45: 1018–1029.

Allelic frequencies for lake trout (*Salvelinus namaycush*) samples collected from 27 small lakes or spawning shoals on larger lakes did not show significant annual changes. Levels of genetic variability were in the high range for Salmonidae, with 57% of the loci examined polymorphic (1% criterion) and 4.7% average heterozygosity per locus. Twenty-one percent of the total genetic variability was due to differences between stocks. Highly significant allelic frequency differences were found among allopatric as well as sympatric stocks. Genetic differences among sympatric stocks of Lake Superior indicated a significant degree of genetic isolation among these stocks. Genetic diversity within stocks, as measured by the proportion of polymorphic loci, was larger in stocks from large lakes than small lakes or transplanted stocks from large lakes into small lakes. Geographic patterns in allelic frequencies were observed. Samples from the northwestern range of our study area (upper Great Lakes, northwestern Ontario, and Manitoba) could be distinguished from those of the southeastern range by both allelic frequency differences and the presence or absence of alleles. We suggest that these two geographic ranges were colonized by lake trout that survived in different refugia during the Wisconsin glaciation. Unusual stocks of lake trout were found in three small lakes in the Haliburton Highlands of southern Ontario, with alleles at high frequencies that are rare or absent in most other stocks. We propose that the Haliburton Highlands lake trout originated from a glacial relict stock and survived during the last glaciation isolated from refugia used by other lake trout.

Les fréquences alléliques chez le touladi (*Salvelinus namaycush*) échantillonné dans 27 petits lacs et bancs reproducteurs de grands lacs n'ont pas montré de variations annuelles significatives. Les niveaux de variabilité génétique s'inscrivent parmi les valeurs élevées observées chez les Salmonidae; ainsi, 57 % des loci examinés sont polymorphes (critère fixé à 1 %) tandis que l'hétérozygosité moyenne par locus se situe à 4,7 %. D'autre part, 21 % de la variabilité génétique totale est le résultat de différences entre les stocks. On a noté des différences nettement significatives entre les fréquences alléliques autant parmi les stocks allopatriques que parmi les stocks sympatriques. Les différences génétiques parmi les stocks sympatriques du lac Supérieur révèlent un niveau significatif d'isolation génétique. La diversité génétique au sein d'un stock, telle que révélée par le nombre relatif de loci polymorphes, est plus élevée chez les stocks peuplant de grands lacs ou chez les stocks transplantés de grands lacs à de petits lacs. On a aussi observé des schèmes géographiques des fréquences alléliques. Les échantillons recueillis dans la partie nord-ouest de la zone expérimentale (Grands Lacs supérieurs, nord-ouest de l'Ontario et Manitoba) peuvent être séparés de ceux prélevés dans la partie sud-est d'après des différences des fréquences alléliques ainsi que par la présence ou l'absence de certains allèles. On formule l'hypothèse que ces deux aires de répartition ont été colonisées par des touladis qui ont survécu à la glaciation du Wisconsin dans différents refuges. On a relevé la présence de stocks peu ordinaires de touladi dans trois petits lacs des hautes terres d'Haliburton dans le sud de l'Ontario; ces stocks possèdent des allèles à haute fréquence rares ou absents chez la plupart des autres stocks. On formule l'hypothèse que le touladi des hautes terres d'Haliburton vient d'un stock relictuel qui a survécu à la dernière glaciation dans un refuge isolé des autres refuges utilisés par d'autres souches de touladi.

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The lake trout (*Salvelinus namaycush*) stocks of the Great Lakes region have declined markedly in this century. Native lake trout have become extinct in Lakes Ontario, Erie, and Michigan and many smaller inland lakes and rivers. Only two small remnant native stocks survived in Lake Huron. Lake Superior still supports large self-sustaining populations, but many of its native stocks have also been lost. The decline of the lake trout has been attributed to predation by the parasitic sea lamprey (*Petromyzon marinus*), overfishing (Smith 1968; Lawrie and Rahrer 1972; Christie 1974; Pycha and King 1975), and, more recently, environmental degradation (Dorr et al. 1981). To rehabilitate the lake trout fishery in the Great Lakes, a massive planting program of about 9 million yearlings annually is in progress. Many smaller inland lakes are also planted with hatchery trout.

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Historical records and interviews with fishermen indicate that the lake trout of the Great Lakes comprised a wide variety of stocks, differing in anatomical features and behavior (Brown et al. 1981; Goodier 1981). Also, physiological and behavioral differences between surviving lake trout stocks have been recorded (Eschmeyer and Phillips 1965; Plosila 1977; MacLean et al. 1981; Horns 1985). In some cases, it was shown that these differences were genetic and were related to local adaptations (Eschmeyer and Phillips 1965; Ihssen and Tait 1974). Differences in growth and survival among planted stocks have also been observed (Plosila 1977; Krueger et al. 1986). Such intraspecific differences have now been observed in a number of species of fish (e.g. Shaklee 1983 and references therein), supporting the idea that species are composed of biological subunits that are adapted to local conditions (Billingsley 1981; Ryman 1981). This concept has important implications for the conservation of genetic fisheries resources and the optimum use of such resources (Loftus 1976; MacLean and Evans 1981; Smith and Chesser 1981). The need to manage species as clusters of genetically distinct populations is particularly relevant to the lake trout in the Great Lakes because they have been altered by excessive exploitation, environmental degradation, and hatchery transplantations. In the Great Lakes alone, about 13 different stocks of lake trout are employed in the rehabilitation program by American and Canadian fisheries agencies. Additional stocks are used in various research and management programs in smaller lakes, especially in Ontario.

Our objective was to use electrophoretic variation at enzyme loci (allozymes) to address a number of issues relating to the genetic variation within and among lake trout stocks. Firstly, by examining variation within geographic samples, we wanted to determine whether lake trout management units, often referred to as stocks, are in fact stocks in the narrower sense of the biological definition. So far, we have used the term "stock" loosely to refer to a management unit, such as a geographically restricted aggregation in a large lake that is regularly harvested, or all the lake trout in a smaller lake. We wanted to test whether such stocks satisfy the conditions of the stock definition "an intraspecific group of randomly mating individuals with temporal or spatial genetic integrity" (Ihssen et al. 1981a). Secondly, by comparing a number of sympatric and allopatric stocks over a broad geographic area, we hoped to gain an understanding of the origins and maintenance of genetic variation among stocks. The study of this second level of genetic variation is meaningful only if the geographic samples approximate biological stocks.

The new genetic diversity information was applied to questions relating to the biology, management, and rehabilitation of lake trout stocks. For example, allozyme data for fish population samples over broad geographic areas have been used to draw inferences about the glacial origin of stocks (e.g. Franzin and Clayton 1977). We wanted to see whether our data could provide any evidence that the lake trout of the Great Lakes area originated from more than a single glacial refugium. An important management question is whether there is any genetic isolation among sympatric stocks that make up the populations of large lakes. If there is genetic isolation, then such populations should not be managed as single units (Shaklee 1983). We used comparative data on genetic differences between allopatric and sympatric stocks to look at this question. An issue relating to lake trout rehabilitation is whether any loss in genetic diversity has occurred in intensively managed stocks, such as transplanted stocks, compared with relatively undisturbed stocks. Since genetic diversity may depend on stock size, data on the genetic diversity for stocks of different sizes are needed to address this question. Loss of genetic diversity, as measured by the reduction of the number of polymorphic loci or the average heterozygosity per locus, has been observed in hatchery fish populations (e.g. Allendorf and Phelps 1980; Ryman and Ståhl 1981) and has been implicated in the reduction of fitness in stocks (Kincaid 1983; Leary et al. 1984).

Materials and Methods

Source of Samples

More than 3500 lake trout from 29 spawning populations or hatchery stocks (Table 1; Fig. 1) were analysed for biochemical genetic variation. For 23 of these, samples were taken from adults during their fall spawning aggregation, in most cases over several years. In addition, hatchery-reared yearlings derived from wild egg collections were analysed for nine of these 23 samples. For the remaining six samples, two of which are hatchery stocks (12H, 23H, Table 1), only hatchery-reared fish were analysed.

Twenty-one of our samples originated from stocks in their native habitats whereas six are known transplants (15T, 16T, 17T, 18T, 19T, 21T) or suspected transplants (13T, 14T) that have established self-sustaining populations in their new habitats. The transplants 15T, 16T, and 17T originated from a now extinct river spawning population in the Dog River (Loftus 1958) flowing into northeastern Lake Superior (Fig. 1). A transplant in 1958 has resulted in self-sustaining populations in the Mishibishu chain of lakes (T. G. Harrison, pers. comm.). Similarly, the Jenny (18T) and Lewis (19T) stocks resulted from a transplant in 1890 that originated from a now extinct population off Beaver Island in Lake Michigan (Visscher 1983). Our 19T sample was hatchery yearlings reared from eggs originating from Lewis Lake whereas the 18T sample was yearlings produced from a hatchery brood stock which, in turn, originated from a Jenny Lake egg collection. The 21T sample was collected from a self-sustaining stock in the south basin of Killala Lake that originated from a transplant for which the precise origin is not known, but is probably the north shore of Lake Superior (Goddard and Odorizzi 1961). The 13T and 14T samples were collected from lakes that have been heavily planted with hatchery fish of Lake Superior origin. One of our objectives was to assess whether the samples from these two lakes are genetically closer to Lake Superior fish or to other lake trout from lakes in the vicinity of these two lakes.

The 23H hatchery stock originated from egg collections in 1948 by commerical fishermen from Lake Superior reefs in upper Marquette Harbor, Copper Harbor, and a reef east of the Keweena Peninsula (Rybicki and Keller 1978). The 12H hatchery stock was, in part, derived from the 17T stock with a possible addition of a sample collected off the north shore of Lake Superior.

For the stocks 1, 10, 12H, 23H, and 29, additional samples were collected from Lake Ontario. These were hatchery fish planted as yearlings and recovered as adults or juveniles. The identity of these fish could be determined from fin clips or

TABLE 1. Sampling data for biochemical genetic study of lake trout from the Great Lakes region. Lakes of origin arranged in order of longitude.

Stock	Stock No.[b]	Lake of origin (Sanctuary lake)[c]	Lat. N	Long. W	Sample size	Sample type[d]	Sampling years
Seneca	1	Seneca	42°31′	76°50′	95	Y	83, 84
Seneca (Ont.[a])	1	Seneca	42°31′	76°50′	65	A	81, 82, 83
Kingscote	2	Kingscote	45°12′	78°13′	65	A	85, 86
Opeongo	3	Opeongo	45°42′	78°23′	84	A	82, 83, 86
Clean	4	Clean	45°14′	78°32′	137	A	83, 86
Redstone	5	Redstone	45°06′	78°35′	53	A	83, 86
Macdonald	6	Macdonald	45°11′	78°35′	173	A	83, 86
Simcoe	7	Simcoe	44°25′	79°20′	126	A, Y	81, 82, 83
Larder	8	Larder	48°05′	79°40′	81	A	82, 86
Parry Sound	9	Huron	45°22′	80°08′	61	A, Y	80, 81, 82, 83
Manitou	10	Manitou	45°50′	82°00′	132	A, Y	81, 82, 83, 85
Manitou (Ont.[a])	10	Manitou	45°50′	82°00′	224	A	81, 82, 83
Evans	11	Evans	46°30′	82°40′	96	A	85, 86
Hill's Lake	12H	Superior	47°55′	85°12′	34	Y	83
Hills' Lake (Ont.[a])	12H	Superior	47°55′	85°12′	225	A	81, 82, 83
Johnson	13T	Superior	47°55′	85°12′	54	A	83, 86
		(Johnson)	45°16′	78°37′			
Kelly	14T	Superior	47°55′	85°12′	89	A	83, 86
		(Kelly)	45°15′	78°37′			
Katzenbach	15T	Superior	47°55′	85°12′	37	A	86
		(Katzenbach)	48°04′	85°20′			
Mishi	16T	Superior	47°55′	85°12′	68	A	85, 86
		(Mishi)	48°05′	85°21′			
Mishibishu	17T	Superior	47°55′	85°12′	118	A, Y	83, 85, 86
		(Mishibishu)	48°05′	85°25′			
Jenny	18T	Michigan	45°40′	85°37′	80	Y	83
		(Jenny)	43°46′	110°43′			
Lewis	19T	Michigan	45°40′	85°37′	74	Y	83
		(Lewis)	44°19′	110°38′			
Michipicoten	20	Superior	47°57′	85°53′	119	A, Y	82, 83, 84
Killala S.	21T	Superior	47°57′	85°53′	93	A, Y	81, 82, 83, 86
		(Killala)	49°05′	86°32′			
Killala N.	22	Killala	49°05′	86°32′	179	A, Y	81, 82, 83, 86
Marquette	23H	Superior	46°31′	86°48′	114	Y	83, 86
Marquette (Ont.[a])	23H	Superior	46°31′	86°48′	285	A	81, 82, 83
Slate Is.	24	Superior	48°40′	87°00′	161	A, Y	80, 82
Nipigon	25	Nipigon	49°50′	88°30′	182	A	83, 84, 85, 86
Keshkabuon Is.	26	Superior	48°32′	88°50′	103	A	85, 86
Hare Is.	27	Superior	48°19′	88°58′	49	A	85, 86
Gull Is.	28	Superior	40°59′	90°19′	64	Y	84, 86
Manitoba	29	Clear	54°05′	101°00′	105	A, Y	82, 83
Manitoba (Ont.[a])	29	Clear	54°05′	101°00′	110	A	81, 82, 83

[a] Yearlings planted into Lake Ontario and recovered as adults.

[b] T refers to transplanted stocks; H refers to hatchery stocks.

[c] Sanctuary lake to which stock has been transplanted.

[d] A = adults; Y = hatchery yearlings.

coded-wire tags. Samples were collected from 1981 to 1984 involving fish planted from 1978 to 1981, inclusive.

Electrophoretic Analyses

For the electrophoretic analyses, either tissue samples (muscle, liver) were collected from wild fish and shipped frozen on dry ice to our laboratory or live fish were transported and analyses performed on fresh or fresh frozen tissue. Three buffer systems (Casselman et al. 1981) were used to score genetic variability for 15 enzyme systems encoded by 28 loci (Table 2). The tissue extraction, horizontal starch gel electrophoresis, and staining techniques have been described previously (Allendorf et al. 1977; May et al. 1979). 4-Methylumbelliferyl phosphatase (MUP) was stained by the method described by May et al. (1980) and observed under ultraviolet light. The genetic nomenclature used to describe loci and allelic variants follows Allendorf and Utter (1979).

To answer the stocks question, we examined genetic variation within samples and among samples from the same geographic sampling location. Tests for departure from Castle–Hardy–Weinberg phenotypic proportions were conducted using a maximum likelihood ratio test (Sokal and Rohlf 1969). For the duplicated loci *Aat-1,2* and *Mdh-3,4*, for which the allelic products of the duplicated loci cannot be differentiated electrophoretically, expected phenotypic proportions were calculated making the usual assumption (e.g. May et al. 1979) of equal

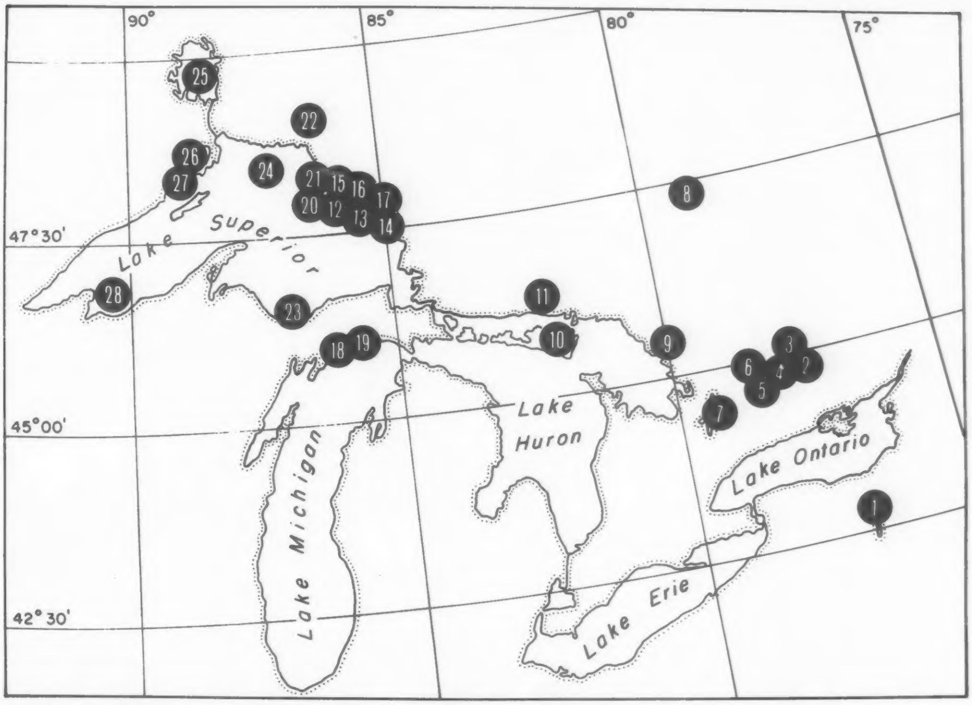

FIG. 1. Lake trout sampling locations and origins of transplanted stocks. For identification of stock by number, see Table 1. For stocks 12, 13, 14, 21, and 23, only the approximate geographic origins are known. Manitoba stock No. 29 not shown.

allelic frequencies at the duplicated loci. Allelic proportions for each locus were compared among repeated samples over years from the same spawning shoal or hatchery stock and between adults and yearlings using maximum likelihood ratios (Sokal and Rohlf 1969). Fisher's exact test was used for samples for which the smallest allelic class had fewer than five alleles. This method permitted us to compare samples without allelic variation at a particular locus with samples having low frequencies at that locus. To examine variation among stocks, standard statistical methods for the analysis of genetic diversity in subdivided populations were used such as average heterozygosity per locus, hierarchical gene diversity, and standard genetic distance (Nei 1972, 1975, 1978).

Results

Out of 28 loci assayed, encoding for 14 enzymes and cathodal muscle protein, 17 were polymorphic (Table 2). We found 12 alleles not previously described in lake trout (Table 2, footnote b). All of these except the *Ldh-4*^{80}, *G3p-1*$^{-70}$, *Pgm-1(0)* (a null allele), and *Pgd*^{85} alleles are at frequencies less than 0.05 in our samples. The new Ldh-4 and Pgd polymorphisms proved to be important for differentiation among the lake trout stocks surveyed in this study. If one considers only those loci polymorphic for which the rarest allele has a frequency >0.05 in at least one sample (5% criterion), then still 13 loci or 46% of the loci examined are polymorphic.

Segregation ratios expected from simple Mendelian inheritance at one or two loci with co-dominant alleles have been found for some of the polymorphisms in our material (Aat-1,2, Sod-2, Mup, Mdh-3,4, Pgd, Gpi-2, Me-1 (P.E. Ihssen, unpubl. data)). For the Mdh-3,4 polymorphisms, the same result has been previously reported in lake trout (Clayton and Ihssen 1980). For the remaining polymorphisms, phenotypes were assumed to reflect genotypes, since the isozyme banding patterns were reproducible and consistent with the known quaternary structure of these enzymes. Further, the genetic basis of these polymorphisms has been confirmed in other species of fish (for a comprehensive study of the inheritance of isozyme variation in salmonids, see May et al. 1979, 1980; Stoneking et al. 1979).

Within-Stock Variability

The tests for deviation from Castle–Hardy–Weinberg equilibrium revealed no more than the expected number of significant results under the null hypothesis except for the duplicated locus Aat-1,2. Four stocks, 4, 5, 6, and 11, have phenotypic proportions that do not fit those expected, if one assumes that both duplicated loci are polymorphic. Only three phenotypic classes were observed instead of the five expected under the assumption of equal allelic frequencies at the two loci. Hence, we postulated that these stocks are polymorphic at only one of these two loci and that the other locus is fixed for the more common allele. For this model, there were no significant differences between the observed and expected phenotypic distributions for all four stocks ($p > 0.7$, maximum likelihood chi-square). Stoneking et al. (1981) were able to account for unusual phenotypic distributions for Aat-1,2 in some brook trout (*Salvelinus fontinalis*) populations with a model than incorporates a null allele. We rejected such a model for our data because it results in significantly fewer heterozygote phenotypes that we

TABLE 2. Lake trout electrophoretic allelic variation.

Enzyme/protein	EC No.	Buffer system[a]	Best tissue	Locus	Variant alleles
Aspartate aminotransferase	2.6.1.1	A	Muscle	Aat-1,2	85[b], 114[c]
Creatine kinase	2.7.3.2	A	Muscle	Ck-1	
		A	Muscle	Ck-2	115[d]
Cathodal muscle protein		A	Muscle	Cmp	
Diaphorase	1.6.4.3	B	Muscle	Dia	
Glycerol-3-phosphate dehydrogenase	1.1.1.8	B	Muscle	G3p-1	−70[d], −187[d]
Glucosephosphate isomerase	5.3.1.9	A	Muscle	Gpi-1	107[d],150[e]
		A	Muscle	Gpi-2	107[d]
		A	Muscle	Gpi-3	
Isocitrate dehydrogenase	1.1.1.42	D	Muscle	Idh-1	
		D	Muscle	Idh-2	
Lactate dehydrogenase	1.1.1.27	A	Muscle	Ldh-1	220[d]
		A	Muscle	Ldh-2	
		D	Liver	Ldh-4	80[d]
Malate dehydrogenase	1.1.1.37	B	Liver	Mdh-1,2	
		B	Muscle	Mdh-3,4	170[f]
Mitochondrial malate dehydrogenase		B	Muscle	mMdh-1,2	
Malic enzyme	1.1.1.40	D	Muscle	Me-1	115[b]
		D	Liver	Me-2	85[d]
4-Methylumbelliferyl phosphatase	3.1.3.2	B	Liver	Mup	−170[e]
Phosphogluconate dehydrogenase	1.1.1.44	B	Muscle	Pgd	85[d]
Phosphoglucomutase	5.4.2.2	B	Muscle	Pgm-1	−110[d],0[d]
		B	Muscle	Pgm-2	−85[g], −112[d],0[c]
Superoxide dismutase	1.15.1.1	A	Liver	Sod-2	85[b]

[a] For description of buffer system, see Casselman et al. (1981).

[b] Dehring et al. (1981).

[c] Leary et al. (1983).

[d] Allele not previously reported.

[e] May et al. (1980).

[f] Clayton and Ihssen (1980).

[g] T. N. Todd (Great Lakes Fishery Laboratory, 1451 Green Rd., Ann Arbor, MI 48105, USA, pers. comm.)

observed and, hence, a poor fit to the phenotypic distributions in our samples.

Two null alleles were found in our samples (Table 2). Since heterozygotes could not be reliably scored for these alleles, allelic frequencies were calculated from the frequencies of homozygotes assuming Castle–Hardy–Weinberg equilibrium (Utter et al. 1984). Heterozygotes are easily missed for null alleles because they differ only in staining intensities of isozyme bands rather than the presence or absence of bands. Estimating allelic frequencies from homozygotes can result in an underestimation of heterozygosity and an overestimation of genetic differences between populations. Hence, null alleles were not used in the analysis of interstock differences.

Allelic frequencies of adults or yearlings and adults sampled in different years from the same spawning shoal, small lake, or hatchery stock were usually not significantly different. Out of 104 comparisons of allelic frequencies, only four were significant ($p < 0.05$) and one at $p < 0.01$ between years. Total chi-square values summed over all polymorphic loci for each of the 25 populations sampled more than once were not significant for 23 ($p > 0.05$) and significant at $p < 0.05$ and $p < 0.01$ for the 24 and 23H stocks, respectively. The 23H sample originated from two hatcheries that obtained their stock from different subsamples of the Marquette hatchery stock. Since there is some genetic variation between year-classes of the 23H stock (Rybicki and Keller 1978), the frequency differences observed were not unexpected. From these temporal sample comparisons and the Castle–Hardy–Weinberg tests, we concluded that these populations can be defined as stocks (cf. Ihssen et al. 1981a).

Different year-classes of the five stocks (1, 10, 12H, 23H, 29) recovered from Lake Ontario as adults from yearling plantings were also found to be homogeneous. However, only a restricted number of polymorphic loci could be analysed because these fish had been in frozen storage several months and, therefore, the electrophoretic patterns for AAT and GPI could not be clearly obtained. Out of 16 allelic comparisons, only one was significant at $p < 0.05$ and none of the total chi-squares over all polymorphic loci for each of the five stocks was significant at $p < 0.05$. Also, the allelic frequencies of these fish were similar to the hatchery stocks from which they originated. Out of 17 allelic frequency comparisons, only two were significant at $p < 0.05$ and none of the total chi-squares over all loci for each stock was significant, except for the stock 23H ($p < 0.05$). This result further supports our earlier contention that this stock is somewhat more heterogeneous than the other stocks.

Among-Stock Variability

A genetic diversity analysis among stocks (Nei 1975) for the 19 wild stocks gave estimates of 0.061 for the total diversity and 0.048 for the average diversity within stocks. Hence, 0.013 or about 21% of the genetic variation is due to interstock differences. These values are similar to interpopulation differences reported for other organisms (Nei 1975). For freshwater fish populations, values such as 31% for smallmouth bass (*Micropterus dolomieui*) (Hallerman et al. 1986) and 39% for bluegills (*Lepomis macrochirus*) (Avise and Felley 1979) have been reported. Generally for marine species, much lower values, such as 2% for Atlantic salmon (*Salmo salar*) (Mork et al. 1985), have been observed. If the hatchery and transplanted stocks are included in our analysis, the interstock genetic variation decreases to 18%. These stocks contribute little additional genetic diversity because most of them originated from Lake Superior and are closely related to some of the other stocks in our sample.

Nei standard genetic distances calculated for 28 loci, including 11 monomorphic loci, ranged from 0.0000 to 0.0717 among the wild stocks sampled. If the hatchery and transplanted stocks are included, the range increases to 0.0000 to 0.0896. These ranges are unusually large for distances among populations of the same species (Nei 1975). In lake whitefish (*Coregonus clupeaformis*), distances among five populations also from the Great Lakes area ranged from 0.0000 to 0.0359 (Ihssen et al. 1981b). The large range observed among the lake trout stocks is primarily due to the samples from the Haliburton Highlands (4, 5, 6). If these samples are omitted, the upper end of the range decreases to 0.0322.

Even for small genetic distances, differences between allelic frequencies of stocks can be statistically significant. For example, the genetic distance between the two stocks 17T and 28 is 0.0003, but the cumulative chi-square over the seven loci that are polymorphic in these two stocks is highly significant ($p <$ 0.01), primarily due to a difference in the allelic frequencies at the Mdh-3,4 locus. Generally, we found that genetic distances greater than 0.0003 were associated with highly significant allelic frequency differences for the sample sizes used here.

Sympatric Stocks

Four of the five stocks sampled from Lake Superior (20, 24, 26, 27, 28) had highly significantly different allelic frequencies at several loci (Ldh-4, Mdh-3,4, Me-2, Sod-2, all with $p <$ 0.01). Only for the two stocks from the spawning shoals of closest proximity (26, 27; ~25 km apart) were no significant allelic frequency differences observed. The shortest distance between the spawning shoals of any of the other stocks is about 150 km (Fig. 1).

The two stocks sampled from the northern and southern basins of Killala Lake also had significant allelic frequency differences. For example, the *Aat-1,2*^{85} allele has frequencies of 0.51 and 0.02 in the northern and southern basins, respectively, and the alleles *Mdh-3,4*^{170} and *Mup*$^{-170}$ are found at frequencies of 0.06 and 0.10, respectively, in the northern basin, but neither allele has been observed in samples of 93 fish from the southern basin (Table 3). The genetic distance between these two stocks was 0.0190, much larger than that for the other sympatric stocks. In general, however, the genetic distances among sympatric stocks are smaller than those among allopatric stocks. For example, the average genetic distance among the native Lake Superior stocks is only 0.0007 compared with 0.0145 for the average of all the stocks in this study.

Allopatric Stocks

Considerable spatial heterogeneity in allelic frequencies and, hence, large genetic distances were observed among allopatric stocks of lake trout. The alleles *Gpi-1*^{150}, *Ldh-4*^{80}, *Aat-1,2*^{114},

TABLE 3. Allelic frequencies for 11 polymorphic lake trout loci. Only the less common allele at each locus is given. Rare polymorphisms: *Gpi-1*^{107}, Opeongo frequency (f) = 0.036; *Gpi-2*^{107}, Manitou f = 0.018; *G3p-1*$^{-70}$, Evans f = 0.036; *G3p-1*$^{-187}$, Seneca f = 0.069; *Ldh-1*^{220}, Slate f = 0.019, Nipigon f = 0.005; *Pgm-1*(0), Evans f = 0.249; *Pgm-2*(0), Jenny f = 0.224; *Pgm-1*$^{-110}$, Nipigon f = 0.005; *Pgm-2*$^{-85}$, Seneca f = 0.008; *Pgm-2*$^{-112}$, Macdonald f = 0.003, Manitoba f = 0.009; *Ck-2*^{115}, Nipigon f = 0.003.

Stock	*Aat-1,2*^{85}	*Aat-1,2*^{114}	*Gpi-1*^{150}	*Idh-4*^{80}	*Mdh-3,4*^{170}	*Me-1*^{115}	*Me-2*^{85}	*Mup*$^{-170}$	*Pgd*^{85}	*Sod-2*^{85}
Seneca	0.280	0.000	0.000	0.000	0.008	0.158	0.000	0.016	0.011	0.000
Kingscote	0.644	0.000	0.000	0.000	0.000	0.000	0.000	0.238	0.000	0.000
Opeongo	0.608	0.000	0.000	0.000	0.000	0.000	0.000	0.006	0.000	0.018
Clean	0.597	0.000	0.000	0.000	0.641	0.000	0.000	0.423	0.357	0.000
Redstone	0.679	0.000	0.000	0.000	0.679	0.000	0.000	0.000	0.000	0.000
Macdonald	0.605	0.000	0.000	0.000	0.685	0.000	0.000	0.558	0.256	0.000
Simcoe	0.232	0.000	0.000	0.000	0.000	0.008	0.000	0.004	0.000	0.008
Larder	0.326	0.008	0.000	0.000	0.000	0.000	0.000	0.130	0.000	0.056
Parry Sound	0.433	0.000	0.000	0.000	0.062	0.066	0.000	0.016	0.000	0.000
Manitou	0.414	0.003	0.000	0.000	0.008	0.034	0.000	0.000	0.000	0.004
Evans	0.611	0.000	0.000	0.000	0.000	0.260	0.000	0.453	0.000	0.000
Hill's Lake	0.412	0.132	0.000	0.000	0.007	0.191	0.000	0.103	0.000	0.000
Johnson	0.431	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Kelly	0.457	0.000	0.000	0.000	0.003	0.006	0.000	0.065	0.000	0.024
Katzenbach	0.368	0.007	0.041	0.000	0.061	0.000	0.000	0.014	0.000	0.122
Mishi	0.412	0.007	0.007	0.000	0.081	0.000	0.000	0.051	0.000	0.103
Mishibishu	0.426	0.000	0.018	0.000	0.072	0.009	0.000	0.030	0.000	0.089
Jenny	0.472	0.044	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.050
Lewis	0.473	0.020	0.000	0.000	0.003	0.000	0.000	0.041	0.000	0.041
Michipicoten Is.	0.469	0.006	0.038	0.056	0.021	0.025	0.034	0.067	0.000	0.004
Killala S.	0.021	0.000	0.011	0.000	0.000	0.000	0.000	0.000	0.000	0.075
Killala N.	0.507	0.012	0.000	0.000	0.058	0.000	0.000	0.095	0.000	0.034
Marquette	0.485	0.054	0.004	0.000	0.024	0.004	0.000	0.061	0.000	0.044
Slate Is.	0.495	0.002	0.006	0.008	0.008	0.044	0.000	0.040	0.000	0.146
Nipigon	0.500	0.027	0.014	0.033	0.010	0.000	0.000	0.054	0.000	0.057
Keshkabuon Is.	0.394	0.000	0.024	0.000	0.000	0.005	0.015	0.039	0.000	0.034
Hare Is.	0.394	0.000	0.020	0.000	0.005	0.010	0.020	0.031	0.000	0.031
Gull Is.	0.430	0.020	0.008	0.000	0.016	0.016	0.000	0.031	0.000	0.055
Manitoba	0.477	0.003	0.143	0.045	0.050	0.000	0.000	0.129	0.000	0.177

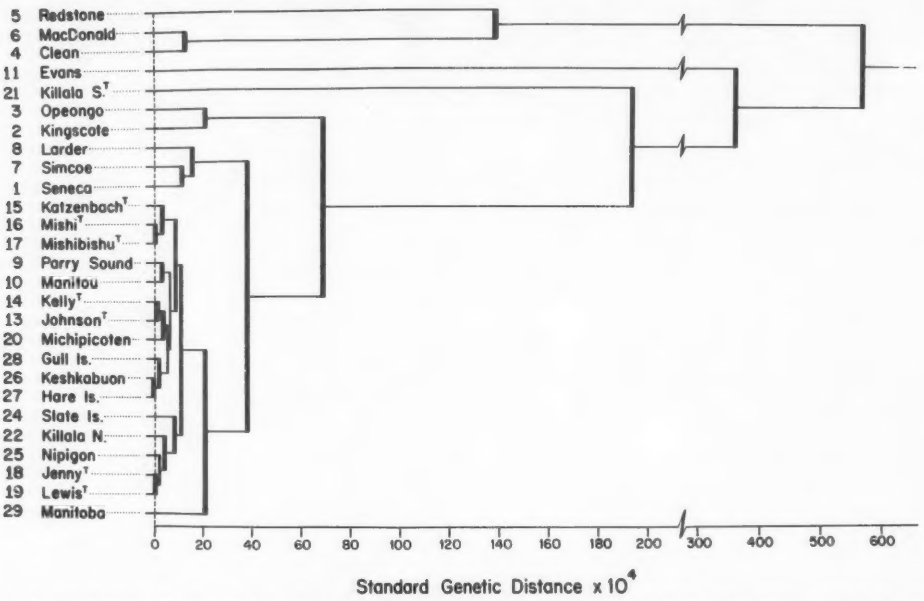

FIG. 2. Dendrogram illustrating the genetic similarity among 27 lake trout stocks including eight transplanted stocks (T). The dendrogram is based on Nei's (1972) standard genetic distance and obtained by UPGMA cluster analysis (Sneath and Sokal 1973).

Me-2^{85}, and *Ldh-1*^{220} were found only in samples from the upper Great Lakes and Manitoba and not in hundreds of fish sampled from southeastern Ontario or northern New York State (Table 3). On the other hand, the allele *Pgd*^{85} has been found only in southeastern Ontario and northern New York. Also, the allele *Sod-2*^{85} is found in every population from the upper Great Lakes and Manitoba, but only sporadically and at lower frequencies in samples from southeastern Ontario. More common alleles such as *Aat-1,2*^{85}, *Mdh-3,4*^{170}, and *Mup*$^{-170}$ do not exhibit the same geographic pattern as the less common alleles and have a more uniform geographic distribution. The highest frequencies for *Aat-1,2*^{85} were observed in a narrow area in the Haliburton Highlands in the Algonquin region of central Ontario (2, 3, 4, 5, 6). Just slightly south of this area (1, 7), some of the lowest frequencies for this allele were observed. The remaining polymorphisms are very localized and have been found in only one or two lakes, usually at very low frequencies.

The allelic frequency distribution for the three stocks from the Haliburton Highlands (4, 5, 6) does not fit the geographic pattern observed for the other stocks. These stocks are clustered on a separate branch in a dendrogram constructed from the genetic distances and are far removed even from stocks in the same geographic area such as 2, 3, and 7 (Fig. 2). The average genetic distance of these three stocks to the other lake trout stocks is 0.056, which is unusually large for intraspecific genetic distances (Nei 1975). The alleles *Aat-1,2*^{85}, *Mdh-3,4*^{170}, *Mup*$^{-170}$, and *Pgd*^{85} had the highest frequencies for all the 29 stocks sampled. Furthermore, *Pgd*^{85} is very rare in all the other lake trout examined (two heterozygotes in 2563 fish), but has a frequency of 0.357 and 0.256 in the 4 and 6 stocks, respectively.

A comparison of genetic diversity indices (Table 4) revealed that stocks from the Great Lakes and Lake Nipigon have more genetic diversity in terms of average proportion of polymorphic loci (P) and average number of alleles per locus (N_a) than stocks from small inland lakes. For example, the mean P for the six wild Great Lakes stocks (9, 20, 24, 26, 27, 28) and the Lake Nipigon stock is 0.244 whereas the mean for the small (<5000 ha, Table 4) wild inland lake populations (2, 4, 5, 6, 8, 11, 22) is 0.153, and the difference is highly significant ($p < 0.003$). Medium-sized lakes (1, 3, 7, 10, 29) had diversities intermediate to the small and large lakes ($P = 0.171$).

Lake area (log ha) was correlated with the proportion of polymorphic loci ($r = 0.60$, 16 df, $p < 0.01$). The partial correlation between log lake area and P, corrected for the number of genes sampled from each stock (N_g, Table 4), is 0.63. Hence, the correlation is not simply due to variation in sample sizes. The average heterozygosity per locus (H) did not have the same pattern of variation as P. The small lakes had similar levels of H (mean 0.056) to large or medium-sized lakes (0.049 and 0.045, respectively).

Transplanted Stocks

Transplanted stocks that originated from the same geographic area had similar allelic frequencies and small genetic distances among them. The three stocks 15T, 16T, and 17T that originated from a single transplant from Lake Superior had no significant allelic frequency difference, and genetic distances ranged from 0.0001 to 0.0003. Similarly, the genetic distance between the two stocks 18T and 19T, which originated from a single transplant from Lake Michigan, was only 0.0001. These two stocks have been examined previously for electrophoretic variation by Leary et al. (1983). Very similar allelic frequencies were observed in both studies.

The two stocks 13T and 14T have been included among the transplanted stocks because these two lakes have been heavily planted with hatchery fish. These stocks have a small genetic

TABLE 4. Genetic variability in 29 lake trout stocks. N_g = average number of genes per locus sampled; P = proportion of polymorphic loci (1% criterion); N_a = mean number of alleles per locus (1% criterion); H = average heterozygosity per locus; A = lake area in log ha.

Stock	No.	N_g	P	N_a	H	A
Seneca	1	189	0.214	1.21	0.047	4.15
Kingscote	2	124	0.107	1.11	0.046	2.32
Opeongo	3	166	0.143	1.14	0.039	3.71
Clean	4	263	0.179	1.18	0.078	2.20
Redstone	5	101	0.107	1.11	0.048	3.07
Macdonald	6	329	0.179	1.18	0.074	2.14
Simcoe	7	252	0.071	1.07	0.027	4.87
Larder	8	155	0.143	1.14	0.045	3.56
Parry Sound	9	121	0.214	1.21	0.049	6.78
Manitou	10	260	0.143	1.14	0.040	4.02
Evans	11	182	0.143	1.14	0.047	1.54
Hill's L.	12	68	0.143	1.18	0.063	—[a]
Johnson	13	91	0.071	1.07	0.036	2.18[b]
Kelly	14	161	0.143	1.14	0.042	2.00[b]
Katzenbach	15	74	0.250	1.25	0.054	2.39[b]
Mishi	16	136	0.214	1.21	0.057	2.35[b]
Mishibishu	17	208	0.250	1.24	0.055	2.92[b]
Jenny	18	160	0.107	1.14	0.042	2.70[b]
Lewis	19	148	0.143	1.18	0.043	3.08[b]
Michipicoten Is.	20	227	0.321	1.32	0.055	6.93
Killala S.	21	180	0.107	1.11	0.009	3.38[b]
Killala N.	22	348	0.214	1.25	0.053	3.38
Marquette	23	226	0.214	1.25	0.051	—[a]
Slate Is.	24	313	0.250	1.25	0.054	6.93
Nipigon	25	342	0.214	1.25	0.051	5.65
Keshkabuon Is.	26	198	0.214	1.21	0.043	6.93
Hare Is.	27	98	0.214	1.21	0.043	6.93
Gull Is.	28	128	0.250	1.29	0.047	6.93
Manitoba	29	202	0.286	1.29	0.074	4.46

[a] Hatchery stocks.

[b] Area of lake presently inhabited by transplanted stock.

distance between them (0.0002) and have much smaller genetic distances to the Lake Superior stocks (mean 0.0004) than to native stocks in the same geographic area (mean 0.0035). Also, the origin of all transplanted and hatchery stocks in Ontario that we were able to trace through hatchery and management records was Lake Superior. Hence, it is very likely that these stocks were established from transplanted fish of Lake Superior origin.

Generally, the transplanted stocks had a significant reduction in genic diversity relative to the native stocks from which they originated. For example, the mean proportion of polymorphic loci for eight transplanted stocks originating from the Great Lakes was 0.161 whereas the mean for five stocks from the Great Lakes was 0.250, and the difference was significant ($t = 2.56$, $p < 0.02$). The average heterozygosity was also reduced in the transplants (5.0% Great Lakes stocks vs. 4.2% transplants), but the difference was not significant ($p \approx 0.09$). The transplanted stocks still resembled the Great Lakes stocks from which they originated in most cases (Fig. 2). For example, the average genetic distance between the transplanted stocks 13T, 14T, 15T, 16T, 17T, 18T, and 19T and the five Lake Superior stocks was 0.0006. This distance was much smaller than most of the genetic distances of native inland lake stocks from Lake Superior stocks (mean = 0.0176) and similar to the genetic distances among sympatric Lake Superior stocks (mean = 0.0007). The 21T stock was an exception to this pattern. It had large differences in allelic frequencies relative to the proposed donor stocks from Lake Superior (mean distance = 0.0131) associated with the largest reduction in genic diversity observed for any of the transplanted stocks (Table 4).

Discussion

The genetic variability we observed in our lake trout samples (P = 57%, 1% criterion; H = 4.7%) is in the high range for Salmonidae. Mean values calculated from 26 studies on Salmonidae summarized by Kirpichnikov (1981) were P = 24% and H = 4.6%. The rainbow trout (*Salmo gairdneri*), considered one of the most genetically variable salmonids, has comparable levels of diversity to what we found in lake trout (P = 50%, H = 6.0%; Allendorf and Utter 1979). Considerably lower levels of diversity have been reported for other *Salvelinus* species, e.g. *Salvelinus fontinalis* P = 38% (Wright and Atherton 1970); *S. alpinus* P = 11%, H = 3.6%, *S. leucomaenis* P = 8%, H = 2.4% (Salmenkova and Volokhonskaya 1973). A low value reported for lake trout (P = 12%, H = 1.5%) by Dehring et al. (1981) was hypothesized as being low because a larger number of monomorphic loci than usual were assayed. Also, the lake trout for the Dehring et al. (1981) study came from a much narrower geographic range (Lake Superior stocks only) than ours. Comparing only the loci scored in both studies for samples from Lake Superior, we found P = 29 and 48% for Dehring et al. (1981) and our study, respectively. We observed four additional polymorphic loci (Ldh-1, Ldh-4, Me-2, Gpi-1) and an additional allele at the duplicated AAT locus (*Aat-1,2*^{114}) in our Lake Superior samples.

None of our samples had phenotypic proportions that deviated significantly from Castle–Hardy–Weinberg equilibrium. Further, no significant allelic frequency differences were observed among samples collected in different years from the same small (<5000 ha) to medium-sized (<100 000 ha) lake or the same spawning shoal from the Great Lakes. These results are consistent with our interpretation that small to medium-sized lakes and individual shoals in large lakes are inhabited by single panmictic stocks.

Sympatric Stocks

We observed considerable genetic differences among sympatric stocks from Lake Superior. Such differences can only be maintained if the stocks are at least partially genetically isolated from each other. Under the assumptions of Wright's (1978) island model, the standard measure of divergence among subpopulations (F_{ST}) can be used to obtain a rough approximation of the gene flow among sympatric stocks expressed in number of migrants (Allendorf and Phelps 1981; Gyllensten 1985). The assumptions are that the genetic variation is selectively neutral, that the populations are in equilibrium, and that there are an infinite number of subpopulations. Allendorf and Phelps' (1981) simulations show that F_{ST} for small migration rates is not only largely independent of the population size, but also of the number of subpopulations. For example, their estimates for F_{ST} for 20 subpopulations are very similar to those for an infinite number of subpopulations. Hence, we conclude that if it is reasonable to assume that the genetic differentiation observed is neutral, our value of F_{ST} can be used to obtain at least a rough approximation of the number of migrants exchanged among these sympatric stocks. The essentially stable allelic frequencies we observed between yearlings and adults for several stocks of lake trout recovered from Lake Ontario indicate that, at least in the short term, no strong selection for these allelic variants is occurring. From our allozyme data, we estimated $F_{ST} = 0.018$ for the stocks sampled from Lake Superior. Using Wright's formula $F_{ST} \approx 1/(4Nm + 1)$, where N is the breeding population size and m the migration rate, then Nm (the number of migrants) is equal to 13.6. If any of the genetic differentiation is not neutral, the populations can remain differentiated for a large number of migrants and, hence, our value may be considered a lower bound. Gyllensten (1985) made similar calculations under the same assumptions using data from the literature for six marine, four anadromous, and nine freshwater species. Estimates for the number of migrants from average values of F_{ST} over species were 15, 6, and 0.6 for the marine, anadromous, and freshwater species, respectively. The low value for local stocks of freshwater fish is expected, since most of these are allopatric and little genetic exchange is possible. The value for marine species (15) is very similar to ours for sympatric Lake Superior stocks (13.6), indicating that freshwater stocks in large lakes interact genetically similarly to local marine stocks.

Estimates of the breeding size of the populations are required to determine the migration rates from the number of migrants. Approximations, based on tag recaptures and the number of adults that are harvested from these stocks, range from 15 000 for the 28 stock to about 20 000 for the 26 and 27 stocks. These results indicate that the migration rates among sympatric stocks of lake trout in large lakes are very low and, hence, that such stocks are essentially genetically isolated from each other.

The very precise homing necessary for the genetic isolation indicated by the biochemical genetic analyses is supported by tagging data for mature lake trout in large lakes. For example, Loftus (1958) found that tagged mature lake trout from a river-spawning population in eastern Lake Superior had a range of only about 50 km. Eschmeyer (1953, 1955) and Rahrer (1968) found that mature lake trout tagged on spawning shoals returned to the vicinity of the tagging site each spawning season. For such tagging studies, a few mature fish are sometimes found at nonnative spawning shoals. However, it is not known whether these fish actually spawn at these sites or whether their presence is simply a phenomenon observed for Pacific salmon, called "proving behavior." Proving fish are thought to be inspecting a nonnative shoal but subsequently seek out their native shoal to spawn.

Our data suggest a resolution to the apparently contradictory results from lake trout homing studies discussed by MacLean et al. (1981). For medium-sized lakes, such as Lake Opeongo (~5000 ha), considerable straying of mature lake trout among spawning shoals has been observed. Such lakes are much smaller in total area than the home range of lake trout stocks in large lakes such as Lake Superior. From tagging studies and biochemical genetic data, we conservatively estimate the home range at about 300 000 ha (a circle with a 30-km radius). This estimate is based on the observation that samples from spawning shoals in Lake Superior less than 30 km apart (26, 27) have the same allelic frequencies and stocks from shoals more than 100 km apart have different allelic frequencies. Also, tagging data indicate that the vast majority of adults do not move more than 100 km from their spawning shoals, but considerable numbers are observed at distances up to 50 km. Hence, it is expected that for lakes much smaller than 300 000 ha, significant movement of adults occurs among shoals that are only a few kilometres apart.

The stocks sampled from spawning shoals in the northern and southern basins of Killala Lake represent a special case. The spawning shoals are at most 15 km apart and the two basins are connected by a short, narrow, navigable channel that permits access of lake trout to both basins throughout the seasons. Killala Lake was fished commercially from 1934 to 1941 for native lake trout. In the 1950's, lake trout of Lake Superior origin were introduced in the lake (Hector and Blackman 1975). Since the 1960's, spawning aggregations have been observed in both basins of the lake. The fish on the northern basin spawning shoal have the appearance of the native lake trout that have been traditionally observed in Killala Lake whereas the fish on the southern basin shoal are larger at the same age and are very different in coloration (Sager 1981). Our samples collected during the spawning season from the two basins were genetically very different. Hence, we conclude that this lake is occupied by two reproductively isolated stocks. Ryman et al. (1979) noted a similar genetic isolation and morphological differentiation for two brown trout stocks occupying two Scandinavian lakes connected by a narrow channel.

Allopatric Stocks

We observed less genetic variability in stocks from small lakes compared with large lakes. Generally, large lakes are inhabited by larger populations of lake trout than small lakes. For example, estimates of the number of adults for small lakes (<5000 ha) range from 1000 to 5000 whereas population estimates for stocks from large lakes such as 24, 25, 27, and 28 range from 10 000 to 30 000 adults. This relationship is due to the strong correlation between lake area and fish biomass (Hanson and Leggett 1982) which, in turn, is correlated with the number of adults. Hence, we have the observation that the proportion of polymorphic loci is correlated with population size. This result is consistent with population genetic theory which predicts that large populations can maintain higher levels of genetic diversity than small populations (Kimura and Crow 1964: Nei et al. 1975).

A similar result has been reported by McClenaghan and Beauchamp (1986) for 16 isolated populations of California fan palms. Palm trees are similar to aquatic organisms in freshwater lakes in the sense that, unlike terrestrial animals and birds, they form populations that are genetically completely isolated from each other over thousands of generations. McClenaghan and Beauchamp (1986) obtained a strong correlation between the log of population size and the proportion of polymorphic loci ($r = 0.72$, $p < 0.01$) and no correlation with average heterozygosity per locus. Hence, if one assumes that the lake trout population sizes are strongly correlated with lake area, the California fan palm results are completely consistent with our lake trout interpopulation genetic diversity data.

McClenaghan and Beauchamp (1986) proposed that the different result for proportion of polymorphic loci and heterozygosity is due to bottleneck and genetic drift effects. As populations pass through years of very low numbers (bottlenecks), genetic drift will cause the loss of alleles that are at low frequencies (Nei et al. 1975). Since most of the heterozygosity results from alleles that are at intermediate to high frequencies, average heterozygosity per locus is relatively unaffected by such events. Furthermore, bottlenecks are a less likely occurrence in larger populations, explaining the dependency on population size.

Another explanation for the lower levels of polymorphism found in the smaller lakes is that the stocks presently inhabiting these lakes were founded by fewer individuals after the last glaciation. By chance alone, small bodies of water are expected to be colonized by fewer individuals which contribute fewer alleles. This hypothesis is attractive also because it can explain the relatively high levels of heterozygosity for the few loci that are found polymorphic in small populations. The explanation is that few founding individuals can only contribute alleles at intermediate to high frequencies. Allendorf and Ryman (1987) have examined the effects of small numbers of founders and bottlenecks on allelic diversity and heterozygosity. They found, in agreement with our results, a larger effect on the proportion of polymorphic loci than on heterozygosity, supporting the hypothesis that these differences are primarily due to population size effects at the time of founding of these populations.

Ecosystem or community effect may also account for the larger genetic variability in large lakes. Such lakes tend to be more ecologically diverse and have more complex fish communities. Correlation between genetic diversity and ecological diversity has been predicted on theoretical grounds (Levins 1968; Maynard Smith 1970) and also observed empirically (e.g. Johnson 1977; Nevo et al. 1984; Bullini et al. 1986). Further, it has been suggested that there may be relationships between genetic diversity and habitat distribution and niche width (Soule 1973). Larger numbers of alleles may be maintained in populations that, because of their ecological heterogeneity, can maintain larger population sizes or experience fewer bottlenecks. Although, from such correlations, it has been inferred that these alleles are not neutral, it is clear that by the above mechanism, such correlations can be established for neutral alleles as well. Great Lakes lake trout stocks that are essentially isolated from each other when stock sizes are large (i.e. low migration rate) may make a significant genetic contribution to a stock passing through a bottleneck (i.e. high migration rate). Thus, sympatric stocks, even if small in themselves, behave like much larger stocks with respect to genetic diversity contributed by rarer alleles. This mechanism of reintroducing genetic variability via migrants is not available to stocks inhabiting small lakes which are physically isolated from each other and would contribute to the disparity in genetic diversity between stocks from large and small lakes.

We speculate that the loss in genetic variability found in transplanted stocks is due to sampling effects alone, since this loss has occurred in only a few generations. Sex products for such transplants may have been collected from too few individuals to sample most of the genetic variability of the donor stock. It was common practice to establish stocks from much fewer than the 200 or so individuals that have been recommended to minimize the loss of genetic variability (Allendorf and Ryman 1987). Selection in hatcheries probably did not cause much loss of variability during the few generations involved because we observed very stable allelic frequencies for parents and their progeny from transplanted stocks in Lake Ontario. In the future, community effects may have a negative impact on the genetic variability of these transplanted stocks, since all eight examined involve the transfer of fish from large lakes with complex communities (Lake Huron, Lake Superior) to smaller lakes with simpler communities.

Zoogeography

The patterns of allelic frequencies we observed strongly suggest colonization from different refugia even in the narrow geographic area encompassed by this study. Stocks from the upper Great Lakes and Manitoba have a number of alleles not found in samples from southeastern Ontario and New York State. For more widely distributed alleles, there are large frequency differences between these two areas. This geographic separation is also seen in the dendrogram (Fig. 2) where these two groups of stocks are separated on different branches. We concluded, therefore, that the upper Great Lakes, approximately west of the 82nd longitude (Fig. 1), and the southeastern range were colonized by lake trout from different refugia. Elsewhere, it has been argued in agreement with our findings that lake trout from the southeastern part of their distribution in North America originated from a different refugium (Atlantic refugium) compared with those from the northwest (Mississippian refugium, Crossman and McAllister 1986). This result was based, in part, on the distribution of the parasite *Cystidicola cristivomer* in lake trout (Black 1982) and morphological differentiation (Khan and Qadri 1971).

The unusual pattern of allelic frequencies noted for the three stocks from the Haliburton Highlands (4, 5, 6) cannot be easily accounted for by founder effects due to colonization from the same refugia as the other lake trout stocks sampled in this study. It is extremely unlikely that alleles could have been introduced by chance at such high frequencies by founders that had these alleles at much lower frequencies. We speculate that these stocks are a relict of the interglacial period and that they may have survived in a interglacial river independently from the lake trout in the other refugia. Since the Mup^{-170} and Pgd^{85} alleles were not found in the 5 stock, but since it had unusually high $Aat\text{-}1,2^{85}$ and $Mdh\text{-}3,4^{170}$ allelic frequencies similar to the 4 and 6 stocks, we postulate that this stock was founded by the 4 or 6 stock. These lake trout are also morphologically and physiologically different from other stocks (J. M. Casselman and P. E. Ihssen, unpubl. data).

An alternative, less plausible explanation, in our view, for the unusual nature of the lake trout from these three lakes is that they may have become genetically differentiated since the last glaciation and the allelic frequency differences are due to selection. Since these lakes are not very different geologically or ecologically from some of the other lakes in this study, it is expected that similar adaptations would have occurred in stocks from other lakes in our sample. However, no such stocks have been found in our admittedly small sample of lakes of similar character. In another study (Speers 1985) on six lake trout stocks from Algonquin Park, in the same geographic area also, no such stocks were found. The pattern of genetic variability for the loci studied by Speers (1985) fitted well with the general pattern of lake trout genetic differentiation we observed for stocks other than these unusual ones.

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Silica and Phosphorus Flux from Sediments: Importance of Internal Recycling in Lake Michigan[1]

Daniel J. Conley[2]

Great Lakes Research Division and Department of Atmospheric and Oceanic Science, The University of Michigan, Ann Arbor, MI 48109, USA

Michael A. Quigley

Great Lakes Environmental Research Laboratory, National Oceanic and Atmospheric Administration, 2205 Commonwealth Blvd., Ann Arbor, MI 48105, USA

and Claire L. Schelske[3]

Great Lakes Research Division, The University of Michigan, Ann Arbor, MI 48109, USA

Conley, D. J., M. A. Quigley, and C. L. Schelske. 1988. Silica and phosphorus flux from sediments: importance of internal recycling in Lake Michigan. Can. J. Fish. Aquat. Sci. 45: 1030–1035.

Estimated lake-wide sediment fluxes of silica and phosphorus (P) were determined and then compared with other components in the biogeochemical cycle to investigate the importance of sediment regeneration in Lake Michigan. Dissolved silica (Si) and soluble reactive phosphorus (SRP) fluxes from sediments were measured by the incubation of intact sediment cores. Estimated Si flux from sediments can supply 21% of the total mass of silica in the water annually and 26% of the Si used during annual diatom production. By contrast, estimated SRP flux from lake sediments can supply only 4.1% of the mass of total P in the water annually and <1% of the P utilized for annual primary production. Because the internal regeneration of P occurs rapidly in the water column, compared with the much slower regeneration of Si ($0.8 \cdot yr^{-1}$), P can be used many times during an annual cycle whereas Si is used only once. Thus, differences in the supply rates and in the biogeochemical recycling rates of Si and P can lead to seasonal Si depletion in the water mass and influence the outcome of seasonal phytoplankton species succession by limiting Si availability necessary for diatom production.

On a déterminé les flux estimatifs de la silice et du phosphore (P) dans les sédiments lacustres pour les comparer aux autres composantes du cycle biogéochimique afin de déterminer l'importance de la régénération des sédiments dans le lac Michigan. On a donc quantifié les flux de la silice dissoute (Si) et du phosphore réactif soluble (PRS) dans les sédiments grâce à l'incubation de carottes intactes de sédiment. Le flux estimatif du Si peut fournir 21 % de la masse totale annuelle de silice présente dans l'eau et 26 % du Si utilisé au cours de la production annuelle de diatomées. Par contre, le flux estimatif du PRS ne fournit que 4,1 % de la masse annuelle de P total présente dans l'eau et <1 % du P utilisé au cours de la production primaire annuelle. Étant donné que la régénération interne du P a lieu rapidement dans la colonne d'eau par rapport à la régénération du Si plus lente ($0{,}8 \cdot a^{-1}$), le P peut être utilisé de nombreuses fois au cours du cycle annuel tandis que le Si n'est utilisé qu'une fois. Ainsi, les différences entre les taux d'approvisionnement et les taux de recyclage biogéochimique du Si et du P peuvent mener à un appauvrissement saisonnier du Si dans la masse aqueuse et influer sur le résultat de la succession saisonnière des espèces de phytoplancton en limitant la disponibilité du Si nécessaire à la production de diatomées.

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Differences in nutrient availability can influence the outcome of competition between algal species (Tilman et al. 1982). In Lake Michigan, increased phosphorus (P) loading has stimulated diatom growth to the extent that epilimnetic diatom production is now seasonally limited by dissolved silica (Si) availability (Schelske and Stoermer 1971). Therefore, biogeochemical cycles of both P and Si and their influence on phytoplankton community composition warrant consideration.

Studies on biogeochemical cycling of silica have demonstrated that most of the Si incorporated into tests of siliceous organisms (biogenic silica or BSi) must be regenerated annually in order to maintain Si dependent production. In oceans, Wollast (1974) estimated that 99% of all BSi produced is regenerated annually. In Lake Michigan, 95% or more of the mass of Si required to sustain diatom production is recycled on an annual basis (Parker et al. 1977; Schelske 1985). Much of the internal

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[1] Contribution No. 492 of the Great Lakes Research Division and Contribution No. 613 of the Great Lakes Environmental Research Laboratory.

[2,3] Present Address: Department of Fisheries and Aquaculture, 7922 NW 71st St., University of Florida, Gainesville, FL 32606, USA

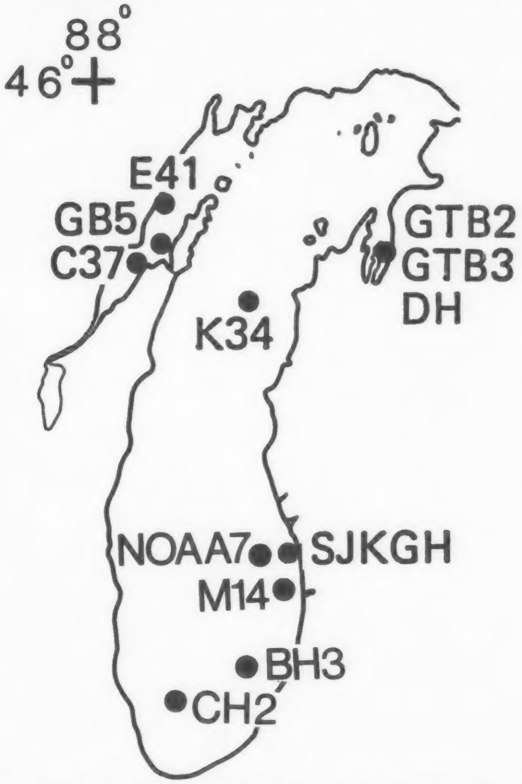

FIG. 1. Stations sampled in Lake Michigan. Stations E41, GB5, and C37 are in Green Bay and stations GTB2, GTB3, and DH are in Grand Traverse Bay.

recycling of BSi is known to result from sediment regeneration (D'Elia et al. 1983; Calvert 1983). However, in Lake Michigan the proportion of internal recycling that occurs in sediments versus the water column has not been determined.

The objective of the present study was to evaluate the importance of Si and soluble reactive phosphorus (SRP) fluxes from sediments for internal cycling of Si and P in Lake Michigan. Areal Si and SRP fluxes were calculated to determine (1) the proportion of Si and P that is regenerated annually from sediments and (2) the importance of sediment flux as a source of Si and P utilized annually for primary production. Differences in the biogeochemical cycling of Si and P and the influence of internal recycling of both nutrients on primary production are discussed.

Materials and Methods

Intact sediment cores were collected from sites in Green Bay and in the open waters of Lake Michigan (Fig. 1). Stations were selected to provide a range of sediment type (Cahill 1981) and to sample different areas within the lake to estimate spatial variability of sediment fluxes.

Sediment cores were collected using a Wildco gravity corer from the *R/V Mysis* and the *R/V Laurentian* in 1983 and 1984, respectively. Cores from stations SJKGH, CH2, and BH3 in 1983 and 1984 were collected using a Kahl Scientific box corer aboard the *R/V Shenenhon*. In 1985, all cores were collected using a Mark IV Soutar box corer aboard the *R/V Laurentian*. Only cores with no visual evidence of disturbance were selected for study.

Estimates of Si and SRP flux across the sediment–water interface were made by incubating intact cores and measuring nutrient concentrations in overlying waters over time. The rate of change of solute concentration in overlying water through time was taken as net release from sediments. Cores for measurement of Si flux were incubated over 24–36 h during the linear release phase (Andrews and Hargrave 1984). Cores used to study SRP flux were incubated over much longer time periods (30–60 d) in order to obtain measurable SRP fluxes (Quigley and Robbins 1986). All cores were incubated in darkness with mild aeration of overlying water to prevent development of concentration gradients. Cores were incubated at 5°C for Si flux and at 6°C for SRP flux. These incubation temperatures were at or near in situ temperatures.

Results and Discussion

Sediment Fluxes

Si fluxes across the sediment–water interface in cores from Lake Michigan ranged from 2.3 to 10.3 mg $SiO_2 \cdot cm^{-2} \cdot yr^{-1}$ (Table 1). The range in Si flux was similar to Si fluxes reported from previous studies on the Great Lakes (see Quigley and Robbins 1984). Because the source of Si flux from sediments is from dissolution of diatom silica, Si flux should be related to sediment concentrations of BSi. Si flux generally increased as a function of BSi concentration in the 0- to 1-cm sediment interval (Fig. 2) and leveled off at higher BSi concentrations as Si flux from sediments becomes limited by diffusion (Conley 1987). A significant fit of a saturation curve to the data from depositional basins was obtained ($r^2 = 0.96$, $P < 0.001$, $n = 23$). Si fluxes from the nearshore station SJKGH were not included in the calculation of the saturation curve because Si fluxes from station SJKGH largely result from the dissolution of a thin layer of BSi on a compacted sediment surface (Conley 1987).

Sediment fluxes of SRP ranged 2 orders of magnitude among all stations (Table 1) and up to a factor of 3 between years at station K34. Sediments incubated from oligotrophic lakes at low temperatures under oxic conditions often have undetectable rates of SRP release, and occasionally sediments show a net sorption of SRP resulting in negative fluxes (Kamp-Nielson 1974; Holdren and Armstrong 1980). Measured SRP fluxes reported here are typical for an oligotrophic, aerobic, cold environment (Nürnberg et al. 1986; Quigley and Robbins 1986).

Si:SRP molar ratios calculated from sediment Si and SRP fluxes were considerably higher than the idealized Redfield ratio for seston of 16:1 (Redfield et al. 1963) and ranged from 460:1 to 6600:1 for ratios that could be calculated (Table 1). Because Si fluxes reported here were in the same range as reported elsewhere, the Si:P ratios were higher due to the relatively low SRP fluxes.

Internal Recycling

The importance of BSi regeneration from sediments can be estimated by computing a lake-wide estimate of Si flux. The lake-wide Si flux from sediments was estimated using the saturation relationship (Fig. 2) to predict sediment Si flux from mean surficial BSi concentrations from different basins (Conley et al. 1986). The predicted Si flux from a particular basin was

TABLE 1. Mean Si and SRP sediment fluxes, standard deviations, and the Si:P molar ratio of fluxes for cores. The number of cores used in the measurement of Si and SRP flux is given in parentheses.

Station	Date	Si flux ($mg\ SiO_2 \cdot cm^{-2} \cdot yr^{-1}$)	SRP flux ($\mu g\ P \cdot cm^{-2} \cdot yr^{-1}$)	Molar Si:P
C37	15 July 83	8.5 ± 0.3 (2)		
	19 July 84	9.1 ± 1.7 (4)	2.46 ± 0.54 (4)	1910
	12 Aug. 85	8.1 ± 2.2 (5)	1.90 ± 2.17 (4)	2210
E41	16 July 83	4.7 (1)		
	19 July 84	6.7 ± 0.9 (5)		
	13 Aug. 85	3.2 ± 0.4 (3)	3.59 ± 0.86 (4)	460
GB5	16 July 83	9.8 (1)		
DH	18 July 83	10.3 ± 0.3 (2)		
	8 Oct. 83	8.7 (1)		
	25 Apr. 84	8.5 ± 0.3 (2)		
GTB2	8 Oct. 83	6.8 (1)		
	25 Apr. 84	3.2 ± 0.9 (3)		
GTB3	8 Oct. 83	7.1 (1)		
	25 Apr. 84	5.1 ± 0.6 (3)		
SJKGH	23 Aug. 83	2.3 ± 0.1 (6)	0.73 ± 0.14 (4)	1620
	4 May 84	4.1 ± 0.5 (3)	0.32 ± 0.51 (7)	6600
	10 Aug. 85	5.3 ± 0.3 (3)		
M14	4 May 84	3.9 ± 0.3 (5)	<0.01 (6)	
K34	20 July 84	8.2 ± 0.5 (5)	1.46 ± 0.80 (8)	2900
	11 Aug. 85	8.8 ± 1.6 (7)	4.55 ± 1.19 (3)	990
NOAA7	20 July 84		1.28 ± 0.26 (8)	
CH2	11 Nov. 84		1.55 ± 0.38 (7)	
BH3	11 Nov. 84		2.16 ± 0.72 (7)	

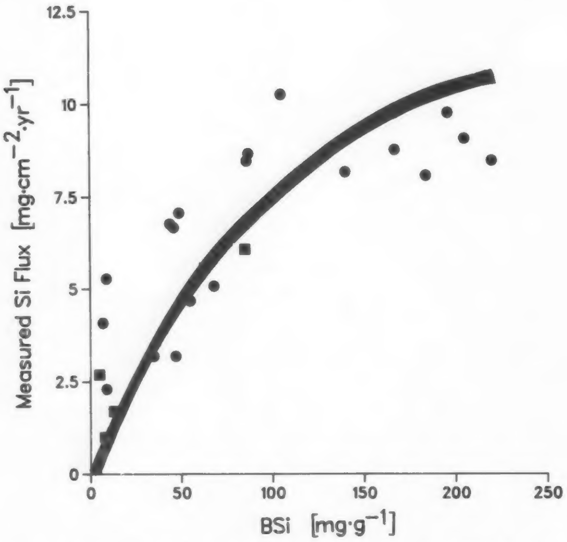

FIG. 2. Measured Si flux vs. BSi concentration in the upper 0- to 1-cm interval in cores. The squares denote unpublished data (C. L. Schelske, unpubl. data). The line is a saturation curve describing the relationship between surficial BSi concentrations and Si flux (K_m = 123, Si $flux_{max}$ = 16.8; $r^2 = 0.96$, $n = 26$)

then multiplied by the basin area (Table 2). Depositional basins released 11.6 × 10^8 kg SiO_2, transitional basins released 1.13 × 10^8 kg SiO_2, and nondepositional basins released 2.10 × 10^8 kg SiO_2 (Table 2). The resulting annual basin-weighted lake-wide Si flux is 14.9 × 10^8 kg SiO_2. A basin-weighted Si flux for Lake Michigan by Schelske (1985), estimated from mean Si fluxes from Great Lakes sediments, ranged from 9 × 10^8 to 13 × 10^8 kg $SiO_2 \cdot yr^{-1}$, or 13–40% lower flux. Schelske's estimated range may be low because it was based on fluxes determined from porewater Si concentration gradients, a method that underestimates Si fluxes in comparison with intact core flux estimates (Conley 1987).

The impact of sediment regeneration on internal system dynamics can be determined by comparing it with other components in the biogeochemical cycle of Si. The total mass of Si in the water column during the winter maximum is 72 × 10^8 kg SiO_2 (Schelske 1985). Therefore, at steady state, on average, 21% of Si in the water is internally regenerated from the sediments annually (Fig. 3). By comparison, tributary inputs of Si are estimated to be 2.0 × 10^8 kg $SiO_2 \cdot yr^{-1}$ (Schelske 1985), only 13% of the sediment flux. Tributary inputs annually supply only 2.8% of the total Si in the water during the winter maximum.

In contrast with Si, SRP fluxes from sediments showed no relationship to surficial sediment total P concentrations, to NaOH-extractable P concentrations in surficial sediments, to depth, or to bulk sediment composition as determined by Cahill (1981). Therefore, for the purpose of calculating an areal SRP flux, it was assumed that SRP fluxes occur at a constant rate over the lake bottom. The mean SRP flux determined from cores, 1.82 ± 1.29 $\mu g\ P \cdot cm^{-2} \cdot yr^{-1}$, was multiplied by the area of the lake bottom. The resulting annual lake-wide estimate of SRP flux from sediments is 1.1 ± 0.75 × 10^6 kg $P \cdot yr^{-1}$. The amount of SRP regenerated from the sediments lake-wide may

TABLE 2. Prediction of areal Si flux for depositional basins, transitional areas, and nondepositional areas in Lake Michigan.

Basin	Area (km^2)[a]	Mean surficial BSi concentration ($mg \cdot g^{-1}$)[b]	Predicted flux ($mg \cdot cm^{-2} \cdot yr^{-1}$)[c]	Basin-wide flux ($\times 10^8$ kg SiO_2)[d]
Depositional basins				
Green Bay	1 620	134	8.8	1.43
Grand Haven	2 030	39	4.0	0.81
Milwaukee	1 450	55	5.2	0.75
Northern	10 300	74	6.3	6.49
Southern	6 900	28	3.1	2.14
Transitional areas	8 700	10	1.3	1.13
Nondepositional areas	26 000	6	0.8	2.08

[a] From Cahill (1981).

[b] From Conley et al. (1986).

[c] Determined from a saturation curve describing Si flux as a function of BSi concentration in the 0- to 1-cm sediment interval (Si $flux_{max} = 16.8$, $K_M = 123$; $r^2 = 0.96$, $n = 23$).

[d] Determined by multiplying predicted basin flux times depositional basin area.

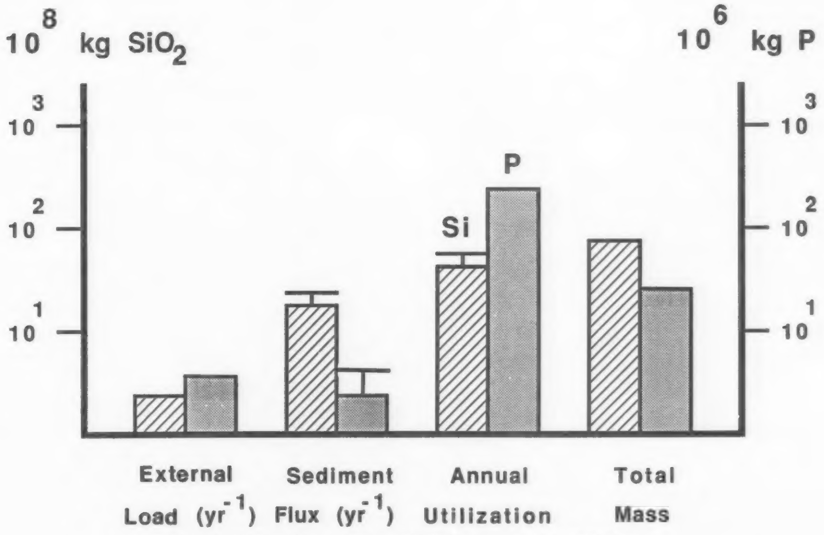

FIG. 3. Comparison of Si and P dynamics in Lake Michigan.

be higher than reported here because Green Bay has periods of reduced oxygen concentrations (Conley 1983), which may lead to increased SRP sediment fluxes (Boström et al. 1982). However, only a small area in Green Bay undergoes oxygen stress during the summer stratified period (<0.6%) relative to total lake bottom (Conley 1983).

Sediment regeneration may be underestimated in this study because high Si and SRP fluxes have been reported from the nearshore environment (Quigley and Robbins 1984, 1986). However, Si and SRP fluxes from cores collected from sandy nearshore sediments may be largely from regeneration within the detrital floc layer (Quigley and Robbins 1984, 1986) which is present only during spring and early summer in shallow water (<15 m) before being resuspended and moved offshore (Nalepa and Robertson 1981). The loss of this material would reduce greatly fluxes of Si and SRP from these sandy sediments and thus reduce the impact of nearshore sediment regeneration.

The importance of lake-wide sediment regeneration of SRP also can be determined by comparing it with other components in the P cycle. The total mass of P in the water column was calculated by multiplying the mean spring open-water column total P concentration of 5.6 μg $P \cdot L^{-1}$ (Lesht and Rockwell 1985) by the volume of the lake, yielding 27 × 10^6 kg P in the water. Thus, internal regeneration of P from lake sediments is only 4.1% of the mass of total P in the water (Fig. 3). By comparison, the total P load to the lake from all sources for the early 1980s was estimated to be 4.1 × 10^6 kg $P \cdot yr^{-1}$ (Lesht and Rockwell 1985), which supplies 15% of the total mass of

P in the water annually and is almost four times greater than the estimated amount regenerated internally from the sediments. The external loading of total P to the lake, therefore, has a greater impact on the mass-balance of P than external loading does on the mass-balance of Si.

Sediment SRP fluxes considered here are mainly those fluxes that originate from release of particle-bound P into porewaters and the subsequent transport across the sediment–water interface into overlying waters. Another source of internal loading is that fraction of sedimented particulate P that is resuspended into the water column. Resuspension of NaOH-extractable P into the euphotic zone measured from sediment traps during the unstratified period is equal in magnitude to the annual input of total P entering the lake from all sources (Eadie et al. 1984). However, resuspended P at deep stations cannot contribute to primary production during the stratified period because P cannot be brought up into the euphotic zone. In Lake Michigan, resuspension is greatest during the winter mixing period (Chambers and Eadie 1981) and might, therefore, control spring total P concentrations. The importance of winter mixing is demonstrated by the fact that when ice cover inhibits winter mixing of Lake Michigan, spring total P concentrations are significantly less than in years without ice cover (Rodgers and Salisbury 1981).

Impact on Primary Production

In order to evaluate the importance of sediment flux of Si, we will compare it with Si utilization required for annual diatom production. Estimated net lake-wide BSi production determined from sediment trap studies and from disappearance of Si in the water ranges from 52×10^8 to 64×10^8 kg $SiO_2 \cdot yr^{-1}$ (Schelske et al. 1984). Therefore, Si flux across the sediment–water interface supplies about 26% of the Si used during annual diatom production. If 5% of annual diatom production is lost to the sediments, the remaining 69% of BSi produced annually must be regenerated elsewhere.

The importance of internal recycling of P for algal production also can be determined. The quantity of P used annually for phytoplankton production was determined indirectly from estimates of primary productivity. Fahnenstiel and Scavia (1987) estimate that 18.3 mg $C \cdot cm^{-2} \cdot yr^{-1}$ is fixed in Lake Michigan. If we use the Redfield ratio for seston, which is 106 C : 1 P (Redfield et al. 1963), then 446 μg $P \cdot cm^{-2} \cdot yr^{-1}$ is used for phytoplankton production, which amounts to 237×10^6 kg $P \cdot yr^{-1}$. The calculated annual P utilization for primary production is thus about 100-fold greater than estimated SRP sediment flux and 57 times greater than combined external loads of total P (Fig. 3). These data suggest that to sustain primary production, the internal regeneration of P must occur on very short time scales and that the regeneration of P must be largely confined to the water column.

The implication of the differences in the biogeochemical cycling of Si and P arises because nutrient availability can influence the outcome of competition and influence seasonal algal succession. The annual biological turnover of Si in the water by diatom production, estimated by dividing the amount required annually for diatom production by the total mass in the water, is $0.81 \cdot yr^{-1}$. Recycling of BSi is relatively slow because it depends on rates of chemical dissolution compared with the rapid biological turnover of P (Lean et al. 1983). BSi is lost from the mixed layer prior to extensive dissolution because of slow dissolution rates, and the subsequent release as Si occurs at depth in the water or in the sediments (Parker et al. 1977; Schelske et al. 1984). Once the lake stratifies, epilimnetic diatom populations become limited by Si availability (Schelske and Stoermer 1971). Thus, the portion of Si utilized for diatom production in a large, deep lake such as Lake Michigan is an annual event controlled by the thermal cycle.

Because the internal regeneration of P occurs rapidly in the water column, compared with the much slower regeneration of BSi, P can be used many times for phytoplankton production during an annual cycle whereas Si is used only once. Thus, differences in the biogeochemical recycling rates of Si and P can lead to seasonal Si depletion in the water mass and influence the outcome of seasonal phytoplankton species succession by limiting Si availability needed for diatom production. In addition, because external loads supply a larger fraction of P in the water (15%) than of Si (2.8%), relatively small P enrichments could cause Si depletion as the result of increased diatom production and sedimentation. These differences in the rates of recycling and supply of Si and P provide the mechanism for the rapid biogeochemical depletion of Si reported for the Great Lakes (Schelske et al. 1983, 1986).

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Growth of Juvenile Coho Salmon (*Oncorhynchus kisutch*) off Oregon and Washington, USA, in Years of Differing Coastal Upwelling

J. P. Fisher and W. G. Pearcy

Oregon State University, College of Oceanography, Corvallis, OR 97331, USA

Fisher, J. P., and W. G. Pearcy. 1988. Growth of juvenile coho salmon (*Oncorhynchus kisutch*) off Oregon and Washington, USA, in years of differing coastal upwelling. Can. J. Fish. Aquat. Sci. 45: 1036–1044.

Estimated growth rates, condition, and stomach fullness of juvenile coho salmon (*Oncorhynchus kisutch*) caught in the ocean in early summer, when mortality was most variable, were as high in 1983 and 1984, years of very low survival and low early upwelling, as in 1981, 1982, and 1985, years of higher survival and higher early upwelling. Chronic food shortage leading to starvation, poor condition, or slow growth apparently was not the cause of the increased mortality of juvenile coho salmon in 1983 and 1984. Survival of juvenile coho salmon was positively correlated with purse seine catches of fish in June and with early summer upwelling, 1981–85. Hence, year-class success probably was determined early in the summer, soon after most juvenile coho salmon entered the ocean. Spacing of the first five ocean circuli, which was positively correlated with growth rate, was not significantly different for fish caught early in the summer and those caught late in the summer, suggesting that growth rate selective mortality in the ocean was not strong. The increase in mortality in 1983 and 1984 may have been caused by increased predation on juvenile coho salmon due to decreased numbers of alternative prey for predators.

Les taux estimatifs de croissance, le facteur de condition et le contenu stomacal de jeunes saumons cohos (*Oncorhynchus kisutch*) capturés dans l'océan au début de l'été, alors que la mortalité était très variable, ont été aussi élevés en 1983 et 1984, années caractérisées par un taux de survie très bas et une faible remontée hâtive d'eau froide, qu'en 1981, 1982 et 1985, années où la survie était plus élevée et la remontée hâtive plus forte. La pénurie chronique de nourriture menant à la privation, à une mauvaise condition ou à une croissance lente n'a apparemment pas été la cause de la mortalité accrue des jeunes saumons coho en 1983 et 1984. De 1981 à 1985, il y a eu une corrélation positive entre la survie des jeunes saumons cohos et les prises de poisson à la senne coulissante en juin et la remontée d'eau au début de l'été. Ainsi, le succès des classes annuelles a probablement été déterminé au début de l'été, peu après que la plupart des jeunes saumons cohos eurent gagné l'océan. L'espacement des cinq premiers anneaux de croissance en mer, montrant une corrélation positive avec le taux de croissance, n'était pas différent de façon significative pour les poissons capturés au début de l'été et pour ceux capturés tard dans la saison, donnant à penser que la mortalité sélective dans l'océan liée au taux de croissance n'était pas forte. L'accroissement de la mortalité en 1983 et 1984 pourrait avoir été causé par la prédation accrue sur de jeunes saumons cohos en raison d'un moins grand nombre d'autres espèces de proie disponibles aux prédateurs.

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Total numbers of coho salmon (*Oncorhynchus kisutch*) smolts released from hatcheries from southern Washington through California (the Oregon Production Index (OPI) area) increased from less than 10 million in the early 1960's to more than 60 million by the early 1980's (Nickelson and Lichatowich 1984). Abundance of adult fish increased concurrently with increased smolt abundance the previous year until the period 1970–76, when production of adults began to fluctuate independently of the number of smolts released. From 1977 to 1985, production of adults declined despite increased releases of hatchery-reared smolts (Nickelson and Lichatowich 1984; Pacific Fisheries Management Council 1986, their table III-1).

Several hypotheses have been proposed to explain the low survival rates of coho salmon after the mid-1970's. One possible explanation is that the poor ocean conditions in the mid-1970's resulted in low survival rates of juvenile coho. As evidence for this hypothesis, several investigators have shown a positive relationship between coastal upwelling during the spring and summer that juvenile coho enter the ocean and resulting adult abundance the following year (Gunsolus 1978; Scarnecchia 1981; Clark and McCarl 1983; Nickelson 1983; Nickelson and Licahtowich 1984). Nickelson (1986) found that survival of hatchery fish in years of strong upwelling was about twice that in years of weak upwelling and that survival of both hatchery and wild coho was inversely related to sea-surface temperatures during years of strong upwelling. Coastal upwelling from the mid-1970's to 1985, a period of low adult abundance, was generally less than from the mid-1960's to the mid-1970's, when adult production was high (Nickelson 1986).

Another hypothesis is that survival is density dependent; i.e. low survival rates occur when large numbers of smolts are released (McGie 1981; McCarl and Rettig 1983). However, McGie (1984) and Peterman and Routledge (1983) found a nonlinear relationship between number of smolts and resulting number of adults only in low upwelling years, which suggests that any density-dependent mortality may be associated with the ocean environment. Nickelson (1986) reported linear relationships between smolts released and adult production the following year for separate analyses of wild, public hatchery, and private hatchery fish. He concluded that ocean conditions had greater effect on coho survival than density-dependent factors.

Because abundance of adult coho salmon is correlated with strength of upwelling that occurs a year earlier and because the number of precocious males (jacks) returning to hatcheries after only one summer in the ocean is generally an excellent predictor of the production of adult coho (Gunsolus 1978; Pacific Fisheries Management Council 1986, their fig. III-1), ocean conditions during the first summer in the ocean appear to significantly affect survival of juvenile coho salmon. Low primary and secondary productivity in the ocean, leading to less food for juvenile fish, is a logical mechanism for the higher mortality of juvenile coho salmon during years of low upwelling. This reduced productivity in years of low upwelling would be expected to result in slower growth rates, lower fish condition, and increased vulnerability to predation, starvation, or disease (Ricker and Foerster 1948; Parker 1971; Scarnecchia 1981). If this mechanism is important, the larger, faster growing fish should survive at higher rates than smaller, slower growing fish.

To evaluate the linkage between ocean productivity and growth of coho salmon during ther first summer in the ocean, we compare growth rates, condition, and stomach fullness of marked and unmarked juvenile coho caught in the ocean in years of low survival and low upwelling (1983 and 1984) with those in years of higher survival and higher upwelling (1981, 1982, and 1985). We also examine the evidence of size-selective and growth rate selective mortality in the ocean during these years.

Materials and Methods

Collections

We collected juvenile coho salmon in purse seine sets in the ocean off Oregon and Washington in May, June, July, and August 1981, May, June, and September 1982 and 1983, June, July, and September 1984, and from late May through June 1985. Sets were made in the upper 20–30 m about every 9 km along east–west transects from about the 37-m depth contour (27 m in 1985) out to about 40 to 50 km offshore where juvenile salmonids were rare or absent. The transects were generally 37 km (20 nautical miles) apart between the mid-Oregon and northern Washington coasts (southern Washington coast in 1981). See Pearcy (1984), Pearcy et al. (1985), or Pearcy and Fisher (1988) for a detailed description of the sampling. A large part of our study area was within the OPI area.

Ocean Conditions and Survival

We used the mean monthly coastal upwelling indices at 45°N, 125°W (Mason and Bakun 1986) as measures of upwelling intensity and potential ocean productivity that might affect survival, growth, and condition of juvenile coho salmon. An index of survival of juvenile coho salmon in each year was derived by dividing the number of jacks returning to public hatcheries in the OPI area in the fall (Pacific Fisheries Management Council 1987, their table V-5) by the total number of smolts released from public hatcheries earlier in the spring (T. Lichatowich, Oregon Dep. Fish Wildl., Portland, OR, pers. comm.). This jack index was used as a measure of juvenile survival rather than one based on adult catches and escapement because of the exceptionally high mortality expressed by OPI coho salmon during their final year in the ocean during the 1983 El Niño (Pearcy et al. 1985; Johnson 1984; Pearcy and Schoener 1987; Pacific Fisheries Management Council 1986).

Growth of Marked Fish

To estimate growth rates of marked fish, we subtracted mean fork length (FL) of the mark group at time of hatchery release from FL at capture in the ocean and divided by days between release and capture. Certain mark groups of coho released in the Columbia river were sampled during their downstream migration by the National Marine Fisheries Service at river kilometre 75 (Dawley et al. 1985a). Because these data on lengths were collected closer to time of ocean entrance, they were used instead of the lengths at time of hatchery release to estimate growth rates for fish from these groups that were collected later in the ocean. We also estimated weight-specific growth rates of marked coho from the slope of the linear regression of ln (weight at capture/mean weight at release) on days between release from the hatchery and capture in the ocean.

Growth of Unmarked Fish

Two age groups of juvenile coho were found in the ocean off Oregon and Washington during our sampling: yearling fish that had spent one winter in fresh water before migrating to the ocean and subyearling fish that entered the ocean about 6–9 mo after hatching. Most wild and public hatchery coho smolts were yearling fish, while many coho smolts released from private hatcheries on the Oregon Coast were subyearling fish. The majority of yearling fish entered the ocean over a relatively short time period between March and June. A very large fraction entered from the Columbia River between mid-April and late June with a peak in late May (Dawley et al. 1985b, their tables 4–6). However, large numbers of subyearling fish entered the ocean over a more extended period from May through September. These two age groups were distinguished by the spacing of the first 21 scale ridges (circuli). The subyearling smolts, because they experienced accelerated growth in the hatchery, had more widely spaced circuli and thus a greater radius to the 21st circulus. Scales were removed from a consistent area above the lateral line behind the dorsal fin (Clutter and Whitesel 1956) from up to 25 fish per purse seine set. Acetate impressions of the scales were made and magnified 88 times for measurement.

Because yearling fish entered the ocean over a fairly short time period, mostly before our sampling in the summer, we were able to make estimates of mean growth rate of these fish from change in mean length over time. For fish classified as yearlings, we estimated mean growth rates between cruises by change in mean length divided by mean days between cruises. Mean spacing of scale circuli formed during ocean residence was also used as a measure of relative growth rates of unmarked yearling fish caught in the ocean. We had found that scale cir-

TABLE 1. Regressions of FL (mm) on scale radius (mm at 88×) for yearling juvenile coho salmon caught in the ocean.

Year	n	r^2	Regression equation
1981	637	0.91	FL = 1.78(SR) + 32.60
1982	398	0.95	FL = 1.76(SR) + 38.81
1983	336	0.94	FL = 1.80(SR) + 32.42
1984	190	0.93	FL = 1.74(SR) + 39.03
1985	251	0.82	FL = 1.71(SR) + 39.67

culus spacing was positively correlated ($n = 83$, $r = 0.81$, $p < 0.01$) with growth rate for a group of individually marked juvenile coho smolts held for about 60 d in saltwater tanks (unpublished data). We made the assumption that spacing of circuli formed in the ocean was also positively correlated with growth rate in the ocean. Based on a comparison of scales from fish collected during downstream migration or at hatcheries and from fish collected in the ocean, we concluded that ocean entrance occurred at about the same time as the abrupt transition on the scale from narrowly or moderately spaced circuli to widely spaced circuli. We measured the radius to the first, fifth, and last circulus formed in the ocean and calculated mean spacing of the first five and all ocean circuli for yearling fish caught in each cruise.

Condition

Fish were frozen at sea individually in marked plastic bags to prevent dehydration and later weighed in the laboratory. Weight was compared with FL measured at sea to determine the weight–length relationships in each year.

Stomach Fullness

We removed stomachs from about 10 fish from each purse seine set and weighed the contents to the nearest 0.1 g. Mean weight of stomach contents as a percentage of total body weight was then determined for each cruise in order to make between-year comparisons. Since sets were made mainly during daylight hours on all cruises of each year, diel fluctuations in feeding should not bias between-year comparisons of stomach fullness.

Growth of Jacks

Growth rates of marked precocious males (jacks) returning to the Anadromous, Inc. facility at Coos Bay, Oregon, between 1980 and 1985 were estimated from the differences between mean lengths at release and return. We also compared mean lengths of jacks returning to Fall Creek and Siletz hatcheries on the Oregon coast between 1978 and 1985 with survival and upwelling in each year.

Selective Mortality

If large ocean entrants survived at a higher rate than smaller ocean entrants, then there should be a shift to a larger mean length at ocean entrance with time in our samples. We back-calculated FL at time of ocean entrance for yearling coho salmon caught in the ocean from the distance along the scale radius 20° ventrad to the long axis of the scale from the focus to the ocean entrance mark. For each yearling fish, distance to the ocean entrance mark was converted to FL using regressions derived from yearling coho caught in the ocean in the same year (Table 1). Mean FL's at the time of ocean entrance for fish caught in each cruise were compared to see if there was a shift to a larger value with time.

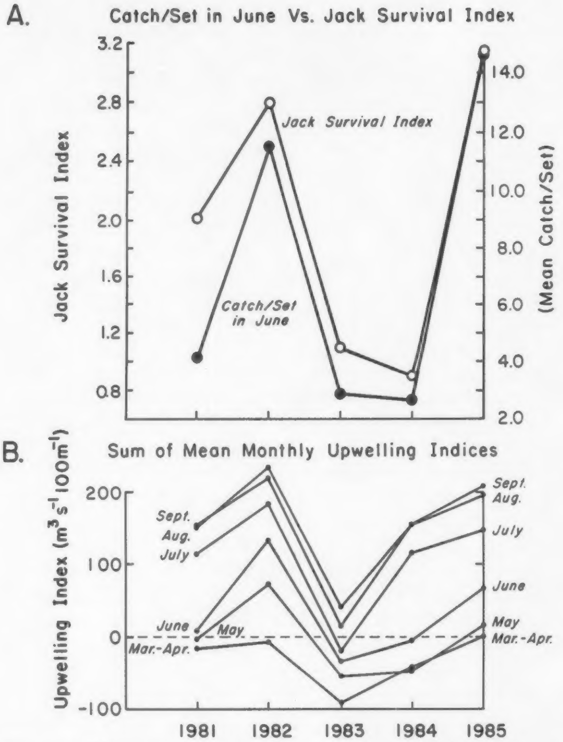

FIG. 1. (A) Mean catch per set in June of yearling juvenile coho salmon vs. jack survival index (see Materials and Methods); (B) sum of mean monthly upwelling indices at 45°N latitude from March through September.

We also back-calculated length at ocean entrance for marked fish sampled during downstream migration in the Columbia River and later caught in the ocean. We compared back-calculated length at ocean entrance for each fish with mean length for the same mark group when sampled during downstream migration in the Columbia River (Dawley et al. 1985a). Consistently larger back-calculated lengths at ocean entrance than mean lengths during downstream migration would indicate that size-selective mortality or growth had occurred between sampling in the river and ocean entrance.

If fish that grew rapidly after entering the ocean survived at a higher rate than those that grew more slowly, then the proportion of the faster growing fish should increase with time. Since scale circulus spacing appears to be positively correlated with growth rate, there should also be a shift to more widely spaced circuli with time. We compared the mean spacing of the first five scale circuli laid down in the ocean in different cruises to see if spacing increased with time.

Results

Ocean Conditions and Juvenile Survival

The survival of juvenile coho between 1981 and 1985 was highly variable. The index of survival of juvenile coho based on jacks returning to hatcheries 4–5 mo after release varied

TABLE 2. Upwelling index, survival index, and growth rates of marked juvenile coho caught in the ocean (20 d or more after release or after river sampling) in the periods May–June and July–September.

	Lower survival years						Higher survival years								
	1983			1984			1981			1982			1985		
Upwelling index (cumulative)															
March–June	−38			−6			6			131			67		
March–September	40			155			152			232			208		
Survival index	1.14			0.91			2.03			2.78			3.19		
Growth rates ($\mathrm{mm \cdot d^{-1}}$)	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD
May–June catch	12	1.42	0.50	6	0.68	0.27	15	0.91	0.62	34	0.90	0.68	75	0.88	0.47
July–September catch	5	1.22	0.65	12	1.28	0.42	31	1.33	0.46	21	1.70	0.39	—	—	—

threefold between 1981 and 1985 and was highest in 1982 and 1985 and lowest in 1983 and 1984 (Fig. 1A). Mean catch per set of yearling juvenile coho in June along eight transects between 46°40′N and 44°20′N varied more than fivefold between 1981 and 1985 and followed the same trends as the jack survival index (Fig. 1A). Mortality of juvenile coho was apparently variable very early in the summer, before June, within 1 mo of the peak outmigration of coho smolts from the Columbia River (Dawley et al. 1985b), the major source of smolts in this area. Therefore, ocean conditions prior to or during June appear to have a great effect on juvenile survival.

Juvenile survival and abundance in June was correlated with coastal upwelling during these years. Cumulative monthly upwelling indices at 45°N, 125°W (Mason and Bakun 1986) were low during early summer (March–June) in 1983 and 1984 and were much higher in 1982 and 1985 (Fig. 1B). Although low in the early summer, upwelling in 1984 intensified later in the summer. Upwelling during the entire spring and summer (March–September) was lowest in 1983 and highest in 1982. The jack survival index was more strongly correlated with cumulative upwelling between March and June ($n = 5$, $r = 0.86$, $0.05 < p < 0.10$) than with the index between July and September ($n = 5$, $r = -0.01$, $p > 0.50$) (Fig. 1A and 1B).

A similar correlation was found for the survival of hatchery coho salmon in the years 1970–85. Survival from smolt to adult for public hatchery fish was more strongly correlated with the cumulative coastal upwelling index between March and June than between July and September of the smolt outmigration year ($n = 15$, $r = 0.59$, $p < 0.025$ vs. $n = 15$, $r = 0.43$, $0.1 < p < 0.2$, respectively; survival data from R. Kaiser, Oregon Dep. Fish Wildl., Newport, OR 97365; data were excluded for the adult production year 1983 when adult mortality was unusually high). Thus, ocean conditions early in the summer of most years seem to be an important factor determining abundance of adults the following year.

Early Summer Growth Rates

Growth rates of juvenile coho salmon early in ocean life appeared to be as high in the low survival years (1983 and 1984) as in higher survival years (1982 and 1985), based on estimates of growth of marked fish and unmarked yearling fish and from spacing of scale circuli. The mean growth rate of marked fish caught during the early summer (May–June) of 1983, a year of low early upwelling and low survival, was greater than in all other years (t-test, $p < 0.05$, Table 2). In the other poor survival year of 1984, mean growth rate was low, but not significantly lower ($p > 0.05$), than in the better survival years 1981, 1982, and 1985. Similarily, growth rate of unmarked yearling fish between May and June estimated from change in mean length was higher in 1983 ($0.73\ \mathrm{mm \cdot d^{-1}}$) than in 1982 ($0.36\ \mathrm{mm \cdot d^{-1}}$). Moreover, mean length in June 1983 (182 mm) was higher than in the June of any other year (Table 3). Mean spacing of all ocean circuli of juvenile coho caught in May 1983, when survival was very low, was greater (t-test, $p < 0.05$) than for coho caught in May 1981, 1982 and 1985, years of much better survival (Table 4). For fish caught in June, mean spacing of the first five ocean circuli, representing about the first 20–35 d of growth in the ocean (J. P. Fisher, unpubl. data), was very similar in all years (t-test, $p > 0.5$) except in 1984 when the sample size was very low. Mean spacing of all ocean circuli for fish caught in June was also similar in all years, except in the year of highest juvenile survival (1985) when it was lower ($p < 0.05$) than in 1981 or 1982. Thus, evidence is lacking for slower growth of juvenile coho in low survival years during the early summer period when survival of fish is highly variable.

Late Summer Growth Rates

In contrast with the trends in early summer, mean growth rate of tagged coho caught late in the summer (July–September) was significantly greater (t-test, $p < 0.05$) in 1982, the year of highest March–September upwelling and moderate juvenile survival, than in other years (Table 2). The mean growth rate in 1982 ($1.70\ \mathrm{mm \cdot d^{-1}}$) was 39, 33, and 28% higher than in 1983, 1984, and 1981, respectively. Mean growth rate of marked fish caught in late summer of 1983 was not significantly different (t-test, $p < 0.05$) than growth rates of those caught in late summer of 1981 or 1984, despite much higher March–September upwelling in these later two years. Growth rates estimated from change in mean length of yearling coho between June and August or September were also higher in the good survival year 1982 ($1.76\ \mathrm{mm \cdot d^{-1}}$) than in the years of low juvenile coho survival 1983 and 1984 (1.37 and $1.33\ \mathrm{mm \cdot d^{-1}}$, respectively, Table 3). Similarily, mean spacing of all ocean circuli for fish caught in August or September of 1982 and 1981 was greater than in 1983 and 1984, years of low survival (t-test, $p < 0.05$, Table 4).

TABLE 3. Mean FL (mm), capture day (May 15 = day 0), and estimated growth rate between cruises for unmarked juvenile coho classified as yearlings.

Year	Cruise	FL			Mean day of capture	Estimated growth rates ($mm \cdot d^{-1}$)			
		n	$\bar{x}$	SD		May–June	June–July	July–Aug. or Sept.	June–Aug. or Sept.
Higher survival years									
1981	May	305	153	16.4	4	1.17	0.97	2.20	1.56
	June	141	180	35.0	27				
	July	97	211	49.9	59				
	Aug.	101	277	44.9	89				
1982	May	132	159	21.1	16	0.36			1.76
	June	197	164	29.8	30				
	Sept.	96	312	36.7	114				
1985	May	234	156	21.2	17	1.27			
	June	256	175	25.1	32				
Lower survival years									
1983	May	116	163	23.6	8	0.73			1.37
	June	145	182	32.0	34				
	Sept.	78	305	26.9	124				
1984	June	37	162	26.2	25		1.33	1.32	1.33
	July	72	226	34.0	73				
	Sept.	82	276	27.3	111				

TABLE 4. Mean spacing of the first five ocean circuli and all ocean circuli for marked and unmarked fish classified as yearlings.

	Month of capture in the ocean								
	May			June			August or September		
	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD
First five ocean circuli									
Higher survival years									
1981	1	2.63	—	36	3.83	0.94	99	4.24	0.95
1982	6	3.11	0.92	24	3.79	0.50	96	4.05	0.68
1985	7	3.31	0.44	52	3.75	0.62			
Lower survival years									
1983	7	3.72	0.94	48	3.78	0.66	79	3.90	0.82
1984				2	3.13	0.00	79	3.72	0.58
All ocean circuli									
Higher survival years									
1981	21	3.16	0.86	65	4.05	0.69	99	4.16	0.47
1982	23	3.21	0.87	51	3.99	0.66	95	4.15	0.39
1985	48	3.29	0.65	118	3.73	0.72			
Lower survival years									
1983	23	3.80	0.97	67	3.86	0.58	78	3.91	0.37
1984				9	3.93	0.50	79	3.95	0.44

Growth in Weight

Instantaneous growth rates in weight of marked juvenile coho salmon in 1983 and 1984 were 2.3 and 2.2% of body weight per day, respectively, rates as high as in 1982, 1983, and 1985 (Table 5). Fish caught both in early and late summer are included in these regressions.

Growth Rate and Size of Jacks

Jacks returning in the fall (September–November) to Coos Bay (Anadromous, Inc.) and the Fall Creek and Siletz hatcheries were smallest in 1983, the year of lowest March–September upwelling, 1978–85 (Table 6). Mean growth rates of jacks

TABLE 5. Growth in weight of ocean-caught marked juvenile coho, where w1 = mean weight at release, w2 = weight of fish when collected in the ocean, and d = days between release and recovery.

Year	Equation	n	r^2
1981	$\frac{w2}{w1} = 0.88e^{0.023(d)}$	76	0.63
1982 (all mark groups)	$\frac{w2}{w1} = 0.90e^{0.020(d)}$	83	0.64
1982 (Columbia R. only)	$\frac{w2}{w1} = 0.68e^{0.026(d)}$	47	0.86
1983	$\frac{w2}{w1} = 1.02e^{0.023(d)}$	38	0.81
1984	$\frac{w2}{w1} = 0.83e^{0.022(d)}$	21	0.72
1985	$\frac{w2}{w1} = 0.98e^{0.015(d)}$	92	0.48

returning to Coos Bay were also lower in 1983 than in all other years. Although survival, as measured by the percent of the smolts released returning as jacks, was very low in both 1983 and 1984 at the Fall Creek and Siletz hatcheries, mean length at both hatcheries in 1984 was as great or greater than in any other year (Table 6). Perhaps the large size of jacks in 1984, relative to 1983, was the result of the much higher upwelling that occurred late in the summer of 1984. The March–September cumulative upwelling index was 150 in 1984 versus only 40 in 1983 (Table 6). Interestingly, unlike for jacks, growth rates for marked and unmarked juvenile coho in 1983 and 1984 were very similar (Tables 2 and 3). Perhaps the large size of jacks in 1984 was due to a late summer growth spurt, after the end of our ocean sampling in September for juvenile fish.

Condition and Stomach Fullness

Fish collected in the poor survival years (1983 and 1984) showed no signs of starvation. Condition (K) in 1983 and 1984 was as high as in the better juvenile survival years 1981, 1982, and 1985 (Table 7). Additionally, weight of food as a percentage of body weight was significantly higher (t-test, $p < 0.05$) in May 1983 than in May 1985 and in September 1983 than in September 1982 or 1984 (Table 8). Although mean stomach content weight was lower in June 1983 than in June 1982, the difference was not significant ($p > 0.05$); however, there was a significant difference between June 1983 and 1985 ($p < 0.05$). Food was apparently as available in 1983 as in the higher survival years of 1982 and 1985. In all years and months, stomach content weight as a percentage of body weight was higher than that reported by Healey (1980) for coho in the Strait of Georgia caught between July and September.

Size-Selective Mortality

Back-calculated lengths at ocean entrance were significantly higher in June than in May 1983 and in August than in May, June, or July 1981 (t-tests, $p < 0.01$, Table 9). These differences could be a result of size-selective mortality: the larger fish entering the ocean surviving at a higher rate causing a shift to a larger mean length at ocean entrance among fish caught later in the summer. However, the back-calculated length at ocean entrance for fish caught in September 1983 was the same as in May, suggesting that the increase in mean length seen in June may have been an artifact. There was no trend for significant ($p < 0.05$) increases with time in back-calculated lengths at ocean entrance in 1982, 1984, or 1985. Hence, consistent differences indicating size-selective mortality were lacking.

Average back-calculated length at ocean entrance of marked Columbia River coho in 1982 and 1983 was slightly greater than mean lengths of these same tag groups when sampled during downstream migration at river kilometre 75 (1982: $n = 22$, $\bar{x} = 5.8$ mm, SD = 5.9; 1983: $n = 8$, $\bar{x} = 7.1$ mm, SD = 7.9 mm). These differences in size could have resulted from size-selective mortality, but they could also have resulted from estuarine growth or a bias in back-calculation of length at time of ocean entrance. Over 90% of coho sampled in the Columbia River had some food in their stomachs and the stomachs averaged half full (Dawley et al. 1986), so it is likely that growth occurred during downstream migration. Average downstream migration rates ranged from 6 to 30 km·d^{-1} (Dawley et al. 1985a), so about 2–11 d of growth could occur between river kilometre 75 and the ocean.

There is little evidence that fish that grew fastest immediately after ocean entrance had higher survival. If this was the case, then mean circulus spacing of the first few ocean circuli should be greater for fish caught late in the summer than for fish caught early in the summer. However, among fish caught in late summer (August or September), spacing of the first five ocean circuli, representing the first 20–35 d of ocean growth, was not significantly different than mean spacing of all ocean circuli

TABLE 6. Growth rates of jacks returning to Coos Bay and mean lengths of marked jacks from releases in March and percent of the release returning as jacks to two coastal Oregon hatcheries in years of varying strength of upwelling.

		Coos Bay (Anadromous, Inc.)			Fall Creek			Siletz		
Year	Mar.–Sept. upwelling index	n	Mean FL (mm)	Mean growth rate (mm·d^{-1})	n	Mean FL (mm)	% returning as jacks	n	Mean FL (mm)	% returning as jacks
1978	160				352	444	0.65			
1979	187				32	420	0.20	13	427	0.12
1980	286	126	360	1.38	33	420	0.24	6	430	0.07
1981	152	1335	366	1.62	47	436	0.34			
1982	232	173	346	1.68	27	432	0.06	28	442	0.11
1983	40	157	293	1.25	26	389	0.03	23	395	0.02
1984	155	12	305	1.51	40	474	0.03	50	446	0.04
1985	208	689	368	1.63	246	441	0.12	139	444	0.08

TABLE 7. Fork length vs. weight relationships for ocean caught juvenile coho salmon. K = condition factor = wt (g) × FL (mm)$^{-3}$ × 10^5.

				Predicted weight and K for three fork lengths					
Year	n	r^2	Regression equation	155 mm		230 mm		300 mm	
1981	287	0.98	wt (g) = 1.44×10^{-6} FL (mm)$^{3.39}$	38.9	1.04	147.5	1.21	365.2	1.35
1982	171	0.99	wt (g) = 2.61×10^{-6} FL (mm)$^{3.28}$	40.0	1.07	146.2	1.20	349.5	1.29
1983	146	0.98	wt (g) = 3.02×10^{-6} FL (mm)$^{3.25}$	40.3	1.08	145.6	1.20	345.7	1.28
1984	505	0.99	wt (g) = 2.81×10^{-6} FL (mm)$^{3.27}$	40.0	1.07	145.0	1.19	345.3	1.28
1985	783	0.97	wt (g) = 1.21×10^{-6} FL (mm)$^{3.42}$	38.0	1.02	146.5	1.20		

TABLE 8. Weight of stomach contents as a percentage of body weight for juvenile coho salmon caught in the ocean in different months and years.

	1982			1983			1984			1985		
Cruise	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD
May[a]	136	2.18	1.21	79	2.21	1.20				136	1.50	1.50
June	296	2.60	1.79	144	2.33	1.63	156	2.01	1.63	228	2.72	1.67
July							100	1.21	1.34			
August												
September	138	1.75	1.49	102	2.42	1.87	145	1.63	1.49			

[a] All sets close to the mouth of the Columbia River in May 1985.

TABLE 9. Back-calculated FL (mm) at time of ocean entrance of yearling coho (marked and unmarked combined) caught in the ocean in different months. Data overscored are significantly different (t-test, $p < 0.05$).

	May			June			July			August			September		
Year	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD
1981	296	150	13.4	138	153	16.7	97	151	18.4	100	164	19.6			
1982	130	152	13.7	185	152	14.9							96	156	18.3
1983	114	152	16.8	145	162	14.8							77	149	17.1
1984				37	155	15.6	72	154	19.7				82	154	15.5
1985	95	155	13.4	135	156	17.3									

(mostly five or fewer circuli) for fish caught in June (Table 4). Thus, any growth rate or size-selective mortality probably occurs prior to June, very soon after ocean entrance.

Discussion

The similar interannual variations in catch per set in June and jack survival index suggest that survival of juvenile coho salmon in the OPI area was most variable during a short period during or right after entry into the ocean. During this early summer period, stomach fullness, condition, and estimated growth rates of juvenile coho were as high in the poor survival years of 1983 and 1984 as in the better survival years of 1981, 1982, and 1985. This suggests that the unusually high mortality of juvenile coho in these years was not a direct result of chronic food shortage in the ocean leading to poor condition or starvation.

Low growth rates do not appear to be associated with low survival rates. Although growth rates were lower in late summer of the poor survival years (1983 and 1984) than in the better survival years (1981 and 1982), growth rates in all years (1981–84) of surviving juvenile coho were quite high, exceeding those found by Healey (1980) for juvenile coho from the Strait of Georgia and Mathews and Buckley (1976) for coho from Puget Sound and the Strait of Georgia. Additionally, growth of jacks in the year of low survival 1984 was greater than in many other years of better survival.

Other workers have found that ocean growth rates and survival rates or abundance are not positively correlated. Bottom (1985) found no correlation between total growth during the first summer and winter in the ocean and survival of coho returning to a coastal Oregon lake system in 13 different years. In fact, he found that spacing of the first six ocean circuli and distance to the first ocean annulus on scales were above average in 1983, a year of very low survival. Mathews and Ishida (S.B. Mathews, Fisheries Research Institute, University of Washington, Seattle, WA, pers. comm.) found that growth rates of poorly surviving coho released early in the summer from the Columbia River and Coos Bay were comparable with those for fish that survived at a high rate released later in the summer.

Several authors (Peterman 1984; Rogers 1980; Mathews 1980) found negative correlations between marine growth and abundance of salmonids, suggesting that growth was density dependent. Bottom (1985) suggested that the better than average growth of coho salmon smolts he found in the very poor survival year 1983 may have been due to the large-scale mortality that occurred that year, reducing competition for food. McGie (1984) found that size of adult coho salmon in the OPI area was negatively correlated with density in the years 1957–76, but contrary to expectations if growth were density dependent, both average size and abundance of adult coho salmon were very low in 1983. McGie argued that the very low average size of adult coho salmon in 1983 was caused by the large numbers of juvenile fish surviving the previous fall (the 1982 jack survival index was high) competing for a very limited food supply in the El Niño year 1983. The relatively high growth rates we found for juvenile coho salmon caught in 1983 and 1984 indicate that food supply in these poor survival years was adequate to support good growth for reduced numbers of surviving fish, despite reduced primary and secondary production in the ocean.

Several authors indicated that size-selective mortality can occur for chum (*O. keta*), pink (*O. gorbuscha*), and sockeye salmon (*O. nerka*) (Parker 1971; Healey 1982; West and Larkin 1987). These authors indicated that selective mortality was most intense for a certain size range of fish or during a specific life history period. The size of fish for which they found size-selective mortality was much smaller than the size of a typical coho smolt. However, Mathews and Ishida (S.B. Mathews, pers. comm.) also found that mean back-calculated lengths at release of surviving adult coho salmon released from Coos Bay were 5–10 mm greater than mean lengths at release, suggesting that mortality may have been greater for smaller fish. We found evidence for size-selective mortality of coho salmon in the ocean between May and late summer only in 1981, suggesting that if size-selective mortality occurs, it probably most often occurs before or during May, the period when mortality is usually most variable.

We conclude that the decreased survival of juvenile coho in 1983 and 1984 was not directly the result of decreased food supply leading to starvation, poor condition, or slow growth. Our data indicate that the variable mortality determining year-class success occurs very rapidly during the time that coho smolts are entering the ocean. Growth rates, condition, and stomach fullness of juvenile coho caught in this early summer period were similar in all years. However, the lower primary and secondary productivity indirectly may have caused higher mortality in 1983 and 1984 through increased predation on juvenile coho salmon as they entered the ocean due to decreased abundances of alternative prey for predators. Shifts in ocean currents in years of low upwelling also may have changed the distribution and increased the vulnerability of smolts to predators.

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Accumulation of Cadmium by Rainbow Trout, *Salmo gairdneri*, during Extended Exposure

Michael A. Giles

Department of Fisheries and Oceans, Central and Arctic Region, Freshwater Institute, 501 University Crescent, Winnipeg, Man. R3T 2N6.

Giles, M. A. 1988. Accumulation of cadmium by rainbow trout, *Salmo gairdneri*, during extended exposure. Can. J. Fish. Aquat. Sci. 45: 1045–1053.

Adult rainbow trout, *Salmo gairdneri*, were exposed to 3.6 and 6.4 μg Cd/L for 178 d. Cadmium accumulated most rapidly in gill tissue which became saturated at levels 100-fold higher than controls within 24 and 52 d in the high- and low-metal exposures, respectively. Liver cadmium increased 250- to 400-fold over the test period but accumulation exhibited a plateau between 52 and 129 d followed by a rapid rise by 178 d. Kidney cadmium increased consistently throughout the test period to levels approximately 50- to 100-fold higher than control values. Cadmium in the gut and skin increased 10- and 5-fold, respectively, while no increase was recorded in white muscle. A maximum of 2.1% of the cadmium available in a commercial diet (0.2 μg Cd/g dry food) was accumulated in control fish. Although cadmium was not detected in the urine, urinary zinc excretion was elevated in trout exposed to 6.4 μg Cd/L such that 7 mol of zinc was excreted per 1 mol of cadmium accumulated during the initial 24 d of exposure. The whole-body burden of cadmium increased linearly with time in both treatments with a time constant of 0.366 and 0.554%/d for trout exposed to 3.6 and 6.4 μg Cd/L, respectively.

Des truites arc-en-ciel adultes, *Salmo gairdneri*, ont été soumises à des concentrations de 3,6 et 6,4 μg Cd/L pendant 178 d. Le cadmium s'est accumulé le plus rapidement dans le tissu branchial qui est devenu saturé à des niveaux cent fois plus élevés que chez les poissons témoins en moins de 24 d et de 52 d respectivement dans les cas d'exposition forte et faible au métal. Le cadmium du foie a augmenté de 250 à 400 fois au cours de la période d'essai mais l'accumulation a atteint un plateau entre 52 et 129 d, suivi d'une augmentation rapide, jusqu'au jour 178. Le cadmium des reins a augmenté de façon constante pendant toute la période d'essai pour atteindre des niveaux d'environ 50 à 100 fois supérieurs aux valeurs observées pour les témoins. Le cadmium au niveau de l'intestin et de la peau a augmenté de 10 et 5 fois respectivement, alors qu'on n'a enregistré aucune augmentation dans le muscle blanc. Chez les poissons témoins, il y a eu une accumulation d'un maximum de 2,1 % du cadmium contenu dans une diète commerciale (0,2 μg Cd/g de nourriture sèche). Bien qu'on n'ait pas décelé de cadmium dans l'urine, l'excrétion de zinc dans l'urine était élevée chez les truites soumises à une concentration de 6,4 μg Cd/L de telle sorte que 7 mol de Zn étaient excrétées pour 1 mol de Cd accumulée pendant les 24 premiers jours d'exposition. La charge de cadmium dans tout le corps a augmenté de façon linéaire avec le temps dans les deux traitements, la constante de temps étant de 0,366 et 0,544 %/d pour les truites exposées respectivement à 3,6 et 6,4 μg Cd/L.

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Anthropogenic contamination of the aquatic environment by cadmium has increased substantially in the last several decades (Hiatt and Huff 1975; Hutchinson 1975; Dickson 1980) and resulted in the elevation of cadmium in the tissues of aquatic organisms at all trophic levels (Blood and Reed 1975; Payer et al. 1975; Harding and Whitton 1978; Murphy et al. 1978). Although cadmium can be accumulated to high levels in fish (Kumada et al. 1973, 1980; Singh and Ferns 1978), the temporal patterns of accumulation by whole fish and specific organs are not resolved. Plateaus in cadmium accumulation have been reported in several studies (Cearley and Coleman 1974; Benoit et al. 1976; Calamari et al. 1982) whereas continuing accumulation has been observed in others (Williams and Giesy 1978; Sangalang and Freeman 1979). Since many of the adverse physiological effects of cadmium are observed during initial phases of exposure (McCarty and Houston 1976; Majewski and Giles 1981; Giles 1984) and then disappear, it is possible that changes in the rate of accumulation by specific organs or the whole fish may occur during extended exposure. This study was conducted to investigate time-related changes in the accumulation of waterborne cadmium by rainbow trout, *Salmo gairdneri*, and determine the role of urine as a route for cadmium excretion.

Materials and Methods

Adult rainbow trout of either sex with a mean (± 1 SD) weight of 375 (±92) g and length of 31.0 (±2.2) cm were obtained from the Rockwood Experimental Hatchery, Rockwood, Manitoba, and acclimated to laboratory conditions for 4 mo at 10°C. Twenty fish were placed in each of six 200-L fiberglass tanks with two tanks serving as controls and two tanks used for exposure to toxicant concentrations of 3.6 and 6.4 μg Cd/L. Dilution water or toxicant solution were supplied at a rate of 2 L/min (95% replacement time = 4 h) and fish were fed commercial pellets once daily for 5 d/wk at a rate of 2% body weight/d corrected for growth over the duration of the experiment. A stock solution of $CdCl_2$ (Fisher, reagent grade) containing 100 mg Cd/L was delivered from a Mariot bottle and mixed with dilution water prior to delivery to the exposure tanks. Water temperature was maintained at 10°C for the entire acclimation and exposure period except for the last 3-wk period when the temperature rose to 15°C at a rate of about 0.25°C/d. Detailed chemical characterizations of the dilution water have been published (Giles 1984).

Six days prior to each sampling period, five fish were removed from each treatment, anesthetized in 0.05% tricaine methanesulfonate (Sigma Chemical Co.), and fitted with a catheter into the urinary bladder. The fish were placed in individual holding chambers (Majewski et al. 1979) and returned to their respective exposure tanks for a 6-d period to collect daily urine samples and to monitor cardiac and ventilatory activity, as described by Majewski and Giles (1981). The fish were then individually anesthetized, bled from the caudal peduncle, and immediately dissected to obtain the desired tissues. Gill arches were removed individually and rinsed in distilled water and the filaments removed immediately distal to the gill arch. The stomach and intestine were dissected free of most fatty tissue, split lengthwise, and rinsed free of any contents. The entire liver was removed and the gall bladder discarded. The posterior kidneys were removed by cutting away the associated mesenteries and scooping out the kidney with a blunt spatula. A 2-cm cube of epaxial muscle was removed from the region of anterior insertion of the dorsal fin and the skin removed with care to avoid contamination with loose scales or bone. Samples of skin including scales were obtained from the dorso-lateral samples. In one instance (80-d exposure) the carcasses remaining after removal of the forementioned organs and samples were homogenized in a Waring blender and aliquots removed for cadmium analyses. All tissues were placed in disposable aluminum pans, dried at 80°C under 90 kPa of vacuum for 24 h, weighed, and digested in a mixture of concentrated nitric acid and perchloric acid (5:1, v:v). The digest was slowly heated until the nitric acid evaporated, diluted with water, neutralized with NH_4OH to pH 3–4, and diluted to a final volume of 25 mL with water. The cadmium was extracted with 4 mL of diethylammonium diethyldithiocarbamate (0.5% in butyl acetate) and the extract analyzed by atomic absorption spectrophotometry on a Varian AA5. Recovery of cadmium in this procedure exceeded 99% (R. Hunt, Freshwater Institute, Winnipeg, Man., pers. comm.).

Cadmium concentrations in water were measured biweekly by atomic absorption on unfiltered water samples from each tank. Actual mean (± 1 SE) cadmium concentrations in the control and two treatments were <0.1 (below detection limit), 3.6 (± 0.4), and 6.4 (± 0.5) μg/L, respectively.

Samples of urine were analyzed directly for cadmium and zinc content without digestion or protein precipitation by atomic absorption spectrophotometry using flame or carbon rod atomization.

The results of the tissue analyses were subjected to an analysis of variance (Steel and Torrie 1960) using both arithmetic and log-transformed data. Homogeneity of variance was tested by Bartlett's test. The tissue concentrations of cadmium are plotted as the geometric mean and 95% confidence interval. The effects of cadmium on the cardiovascular–respiratory system and on plasma and urine electrolytes have been reported previously (Majewski and Giles 1981; Giles 1984).

Results

Growth and Dietary Cadmium Ingestion

Growth in weight was not affected by cadmium ($F = 0.1816$, $P < 0.01$). The fish grew at an average rate of 0.51%/d for the first 80 d and 0.10%/d thereafter. The commercial diet contained 0.20 ± 0.04 μg Cd/g (mean $\pm$ 1 SD, $n = 3$). The cumulative ingestion of cadmium from this source (Table 1) was calculated using the feeding rate of 2% body weight/d for 5 d/wk. Cumulative cadmium ingestion increased exponentially with time reflecting the exponential increase in weight and 236 μg of cadmium was potentially available to the average fish over the 178-d experimental period. From estimates of cadmium accumulation in control fish, 4.9 μg or 2.08% of the dietary cadmium was accumulated, assuming the diet was the sole source of cadmium in these fish.

Tissue Accumulation of Cadmium

Analysis of variance of cadmium concentrations in stomach, intestine, liver, kidney, and gill demonstrated highly significant ($P < 0.001$) treatment, time, and interaction effects. Bartlett's chi-square for homogeneity of variance was significant in all cases. ANOVA of logarithmic transformations of cadmium concentration (Table 2) indicated highly significant time and treatment effects for all tissues but reduced the nonhomogeneity of variance in kidney, intestine, and gill and also reduced interactive effects in intestine and gill. For these reasons the temporal patterns of cadmium accumulation in the different organs (Fig. 1–4) are presented as semilogarithmic plots.

Cadmium increased 30-fold in the gills of treated fish during the first 10 d of exposure (Fig. 1), exhibiting an accumulation rate of 32–35%/d (Table 3). Thereafter, the accumulation rate declined drastically and became negative during the last sampling interval. These observations indicate saturation of the sites for cadmium absorption on the gill or the development of an equilibrium between gill absorption and translocation of cadmium to other sites in the body.

Liver cadmium concentrations were about an order of magnitude lower than those of kidney in unexposed trout (Fig. 2, 3). During cadmium exposure, however, cadmium accumulated at a higher rate in liver than in kidney (Table 3), and after 52 d of exposure, both tissues contained approximately 2–4 μg Cd/g. In the interval of 52–129 d, liver cadmium stabilized or declined whereas cadmium continued to increase in the kidney over the entire exposure period. A rapid rise in liver cadmium between 129 and 178 d of exposure resulted in final concentrations which were approximately 50% of those observed in kidney. Over the entire experimental period the highest rates for cadmium accumulation were observed in liver although gill tissue had the highest rate for the initial 10-d period. Exposure to 6.4 μg Cd/L produced higher tissue levels of cadmium than did 3.6 μg Cd/L although the differences were generally not significant when compared at each sampling interval.

Cadmium accumulation in the intestine and stomach (Fig. 4) was similar at both levels of cadmium exposure although during the initial 52 d of exposure the intestine contained metal concentrations which were 1.2–2 times higher than those in the stomach tissue. An analysis (M. A. Giles, unpubl. data) of 10 trout weighing 130–220 g demonstrated that stomach weight as a proportion of total gut weight was 69.6% (95% C.I. 65.4–73.6%). Therefore, accumulation rates for cadmium in the gut (Table 2) were calculated by weighting the stomach and intes-

TABLE 1. Growth and dietary cadmium intake of trout in this study. Wet weights are presented as the mean ± 1 SE for $n = 5$. Cumulative ingestion of dietary cadmium was calculated using the mean weight of all fish sampled at each time. ANOVA of weight; time (6 df, $F = 19.03$, $P < 0.01$), treatment (2 df, $F = 0.18$, NS), interaction (12 df, $F = 1.07$, NS), Bartlett's (χ^2) (20 df, $\chi^2 = 18.72$, NS).

	Exposure time (d)						
	3	10	24	52	80	129	178
Weight (g)							
Control	336.3 ±14.6	349.5 ±21.9	320.8 ±25.7	471.3 ±26.2	554.2 ±46.5	607.7 ±42.5	628.0 ±66.3
Cd (3.6 μg/L)	365.1 ±46.2	343.9 ±15.8	388.9 ±33.1	423.0 ±55.1	534.5 ±39.8	550.4 ±26.6	644.3 ±78.8
Cd (6.4 μg/L)	400.0 ±53.2	353.5 ±28.8	446.6 ±16.5	443.9 ±40.2	538.3 ±48.1	574.9 ±55.8	525.5 ±72.4
Cumulative Cd ingestion							
μg/fish	3.1	10.0	24.5	54.5	90.2	166.1	236.0
μg/kg	8.4	28.6	63.6	122.2	166.3	287.5	393.8

TABLE 2. Summary of F values for time, treatment, and interactions effects of cadmium exposure upon tissue cadmium concentrations and χ^2 values of Bartlett's test for homogeneity of variance.

Source[a]	df	Stomach	Intestine	Liver	Kidney	Gill[b]
Time	6	32.78 (3)	28.13 (3)	21.05 (3)	70.02 (3)	9.09 (3)
Treatment	2	124.69 (3)	38.60 (3)	226.77 (3)	590.72 (3)	935.40 (3)
Interaction	12	6.33 (3)	2.01 (1)	10.43 (3)	35.89 (3)	2.49 (1)
Bartlett's (χ^2)	20	50.64 (3)	22.64 (0)	84.09 (3)	32.12 (1)	10.62 (0)

[a] Levels of significance in ANOVA in parentheses: 0, not significant; 1, $0.01 < P < 0.05$; 2, $0.001 \leq P < 0.01$; 3, $P \leq 0.001$.

[b] df for time = 5, interaction = 10, Bartlett's (χ^2) = 17.

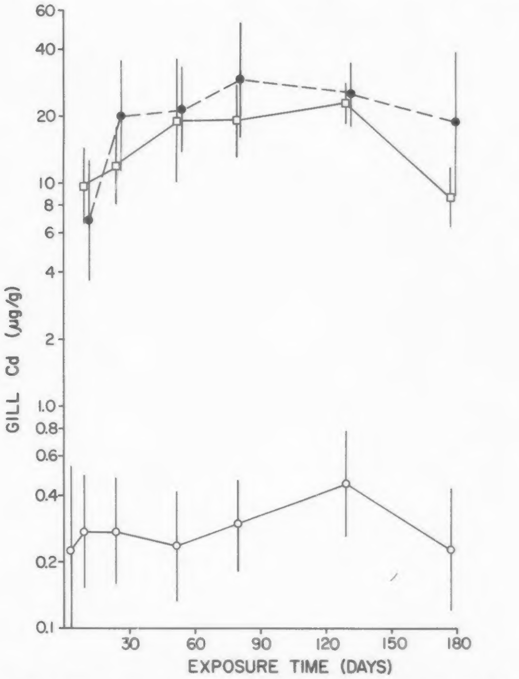

FIG. 1. Cadmium concentration in gills of rainbow trout exposed to 3.6 (□) and 6.4 (●) μg Cd/L and in controls (○). Results are presented as mean and 95% confidence interval for $n = 5$ for dry tissue.

tine concentrations by 0.696 and 0.304, respectively. The negative constant for trout in 3.6 μg Cd/L at 3 d was an artifact arising from the averaging of the highly variable control results. The gut accumulated the least cadmium of all the organs examined but did exhibit a relatively constant rate of accumulation over the experimental period.

Estimates of cadmium in muscle and skin were obtained in trout only after 80, 129, and 178 d of treatment and in carcass (estimated from an aliquot of a homogenate of a tissue remaining after removal of the gut, kidney, liver, gills, and small samples of muscle and skin) only after 80 d of treatment (Table 4). No significant differences were observed in muscle cadmium among controls and treated fish in the three sampling periods. Cadmium was elevated in the skin and carcass of cadmium-exposed fish ($P < 0.05$) but no differences were observed between the two levels of treatment. From these observations a concentration of 0.144 μg Cd/g dry carcass (the average value for cadmium exposed trout at 80 d of exposure) was used in the estimation of the contribution of the carcass to the whole-body burden of cadmium in treated fish.

Urinary Excretion of Cadmium and Zinc

In an attempt to identify possible routes for excretion of metals, cadmium and zinc were measured in the urine of trout after various periods of cadmium exposure. Except for a transitory rise in the initial 3 d of exposure to 6.4 μg Cd/L when two fish exhibited urinary levels of 3 and 4 μg Cd/L, the concentration of cadmium was always less than 0.5 μg/L which was near the limit of detection in the screening method employed. Since these fish produced approximately 65 mL urine·kg^{-1}·d^{-1}, (Giles 1984), the maximum elimination rate of cadmium via

TABLE 3. Rates of cadmium accumulation in the organs of rainbow trout during exposure to 3.6 and 6.4 μg Cd/L. The constants were calculated as $100[\ln[Cd_{t=2}] - \ln[Cd_{t=1}]]/t_2 - t_1)$ and are expressed as %/d.

Time interval (d)	Gill		Liver		Kidney		Gut	
	3.6	6.4	3.6	6.4	3.6	6.4	3.6	6.4
0–3	—	—	32.562	55.051	—	11.198	−6.613	4.077
3–10	35.432[a]	31.893[a]	15.976	8.663	9.577[a]	12.923	8.310	9.797
10–24	1.494	7.784	3.862	5.472	2.975	4.386	2.520	1.558
24–52	1.678	0.196	3.711	3.673	2.869	2.433	2.593	1.513
59–80	−0.013	1.156	−0.060	0.250	3.988	3.674	1.396	−0.101
80–129	0.388	−0.329	−3.336	−1.181	0.729	0.283	0.504	2.135
129–178	−2.039	−0.606	7.019	5.000	1.136	1.839	1.301	1.422

[a] Time interval 0–10 d.

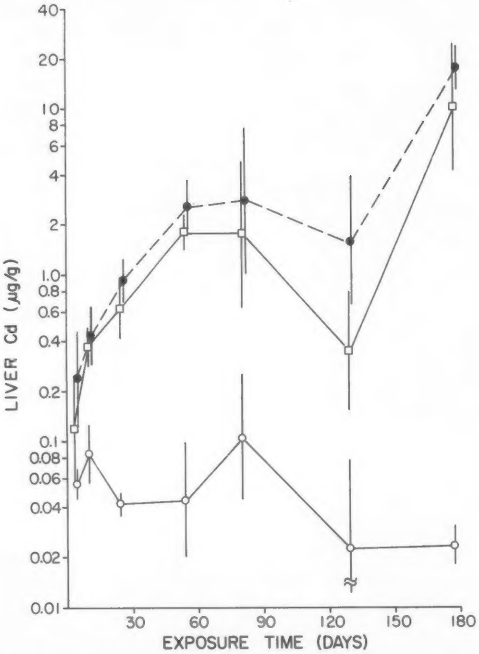

FIG. 2. Cadmium concentration in liver of rainbow trout exposed to 3.6 (□) and 6.4 (●) μg Cd/L and in controls (○). Results are presented as mean and 95% confidence interval for $n = 5$ for dry tissue.

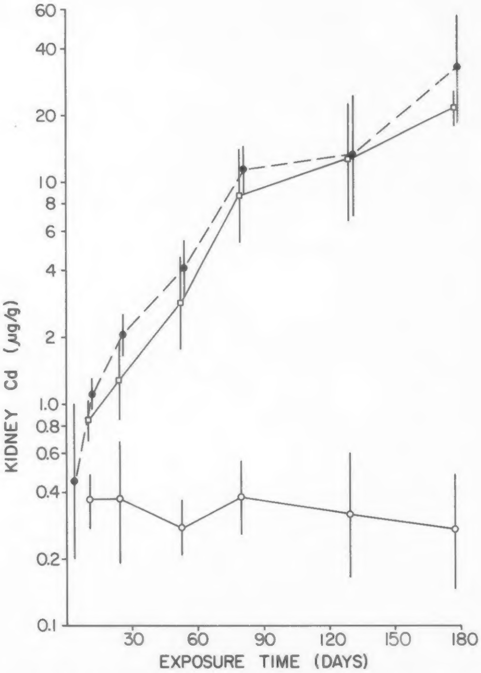

FIG. 3. Cadmium concentration in kidney of rainbow trout exposed to 3.6 (□) and 6.4 (●) μg Cd/L and in controls (○). Results are presented as mean and 95% confidence interval for $n = 5$ for dry tissue.

this route would be 0.033 $\mu g \cdot kg^{-1} \cdot d^{-1}$. This would represent approximately 3.7 and 2.4% of the total cadmium accumulated in trout exposed to 3.6 and 6.4 μg Cd/L, respectively, for 178 d.

The concentration of zinc in the urine of fish exposed to 6.4 μg Cd/L (Fig. 5) was significantly elevated over control levels during the initial 24 d of exposure. Thereafter, no difference was observed among the experimental groups except at 168 d when urinary cadmium was elevated in fish exposed to 3.6 μg Cd/L. Mean urinary zinc excretion in control fish was 1720 $\mu g \cdot kg^{-1} \cdot d^{-1}$ whereas the comparative value for trout exposed to 6.4 μg Cd/L was 4235 $\mu g \cdot kg^{-1} \cdot d^{-1}$ for the first 24 d of exposure.

Body Burden of Cadmium

Assessment of the contribution of the various tissues and organs to the total body burden of cadmium requires an estimate of the relative weight of each tissue. The somatic index (organ weight/body weight) of each organ varies with size. The indices for liver and gut were obtained from the weight-specific relationships calculated by Denton and Yousef (1976), and the kidney index was extrapolated from the relationship presented by Schiffman and Fromm (1959) for juvenile rainbow trout. In fish of the size range employed in this study, liver, gut, and kidney comprise approximately 1.4, 10.5, and 0.9%, respectively, of total body weight. Gill filaments, exclusive of the cartilagenous arch, represent 0.97% (95% C.I. 0.84–1.10%, $n = 10$) of total body weight (M. A. Giles, unpubl. obs.). All calculations of body burden of cadmium (Fig. 6) were based on estimates derived from weights of dry tissue and mean weights of all fish at each sampling interval.

In both treatments the gill cadmium burden equalled approximately 50% of the total burden for the initial 52 d of exposure,

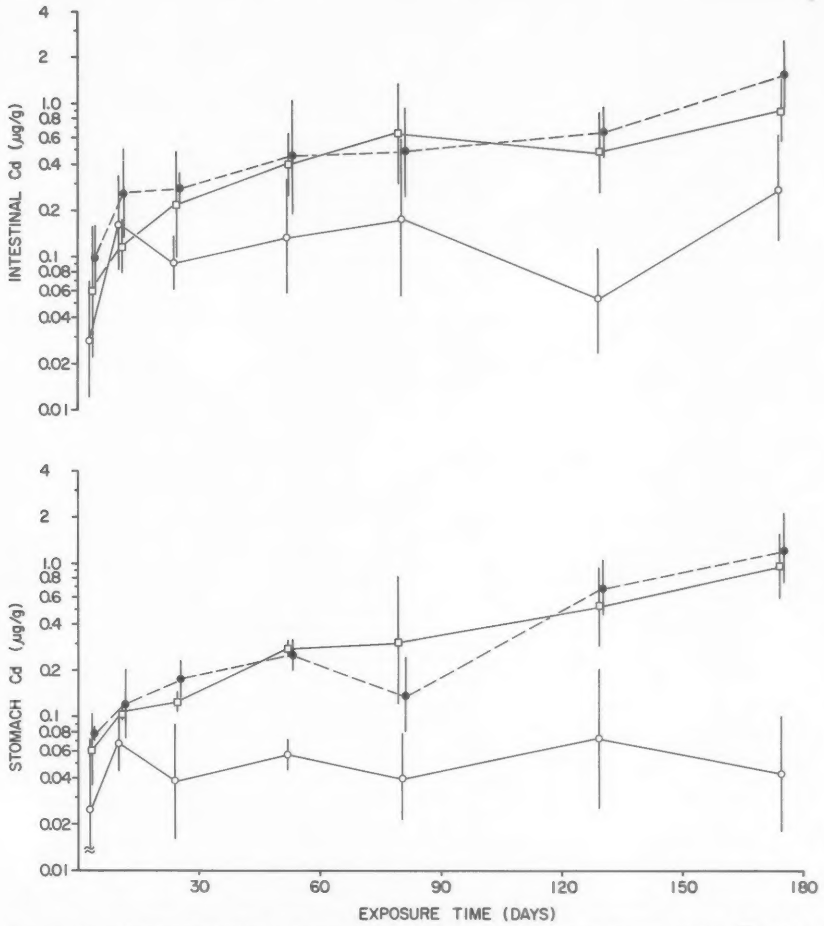

FIG. 4. Cadmium concentration in stomach and intestine of rainbow trout exposed to 3.6 (□) and 6.4 (●) µg Cd/L and in controls (○). Results are presented as mean and 95% confidence interval for $n = 5$ for dry tissue.

TABLE 4. Cadmium levels (µg/g dry tissue) in muscle, skin, and carcass of rainbow trout after extended exposure to dissolved cadmium. Results are presented as the geometric mean and 95% confidence interval (in parentheses) for $n = 5$. Underlined values are not significantly different ($P \geq 0.05$).

Exposure time (d)	Tissue	Control	3.6 µg Cd/L	6.4 µg Cd/L
80	Muscle	0.040 (0.003–0.515)	0.030 (0.011–0.079)	0.020 (0.012–0.036)
	Skin	0.025 (0.014–0.044)	0.132 (0.048–0.363)	0.130 (0.098–0.172
	Carcass	<0.01 (<0.01–0.01)	0.069 (0.048–0.100)	0.125 (0.063–0.249)
129	Muscle	0.101 (0.043–0.241)	0.178 (0.081–0.391)	0.111 (0.066–0.187)
	Skin	0.089 (0.074–0.107)	0.346 (0.217–0.550)	0.573 (0.382–0.861)
178	Muscle	0.032 (0.021–0.050)	0.060 (0.037–0.099)	0.061 (0.040–0.094)
	Skin	0.047 (0.036–0.062)	0.210 (0.137–0.321)	0.232 (0.115–0.469)

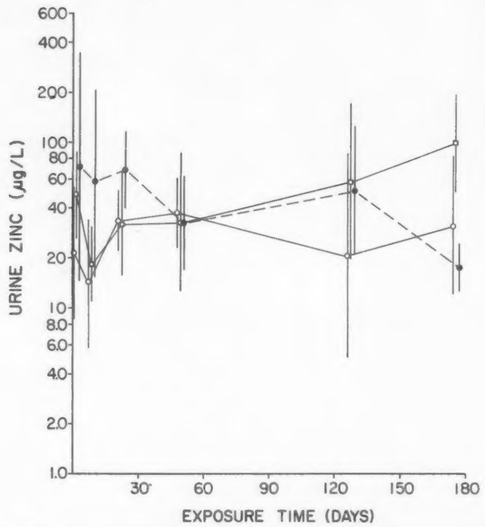

FIG. 5. Zinc concentration in urine of rainbow trout exposed to 3.6 (☐) and 6.4 (●) µg Cd/L and in controls (○). Results are presented as mean and 95% confidence interval.

with liver and kidney each contributing less than 7%. Thereafter, kidney contributed an increasing percentage to the total burden, from 20% after 80 d to 30% after 178 d. The contribution of liver remained at less than 10% until 129 d but increased rapidly to 23–26% after 178 d. In the low-cadmium exposure group, gut cadmium as a fraction of total burden increased progressively with exposure time from 5.5% at day 3 to 17.2% at day 178. In the high-cadmium group, however, the contribution of gut cadmium was unrelated to exposure time up to 80 d but did increase twofold in each of the last two sampling periods.

The total body burden of cadmium increased linearly with time in controls and both treatment groups and was described by the following regression equations:

$$Y(0) = 6.2724 + 0.0276T \qquad R^2 = 0.8111, n = 7$$

$$Y(3.6) = 10.438 + 0.366T \qquad R^2 = 0.979, n = 7$$

$$Y(6.4) = 8.496 + 0.554T \qquad R^2 = 0.958, n = 7$$

where $Y(0)$, $Y(3.6)$, and $Y(6.4)$ is the total content of cadmium per fish in trout exposed to 0.0, 3.6, and 6.4 µg Cd/L, respectively, and T is exposure time in days.

The ratio of total cadmium burden in fish exposed to 6.4 versus 3.6 µg Cd/L was 1.02, 0.92, 1.37, 1.12, 1.27, 1.13, and 1.54 at 3, 10, 24, 52, 80, 129, and 178 d, respectively, showing that the pattern of accumulation at both these toxicant levels was similar throughout most of the test period. In control fish the gut, liver, kidney, gill, and carcass contributed (mean ± 1 SD) 12.3 ± 6.7, 0.9 ± 0.5, 3.5 ± 0.7, 2.9 ± 0.8, and 80.5 ± 5.8% of the cadmium to the whole-body cadmium burdens which increased from 6.3 to 11.2 µg/fish over the experimental period. No change in the functional contributions of the various tissues to the whole-body cadmium burden of control fish was observed during the course of the study.

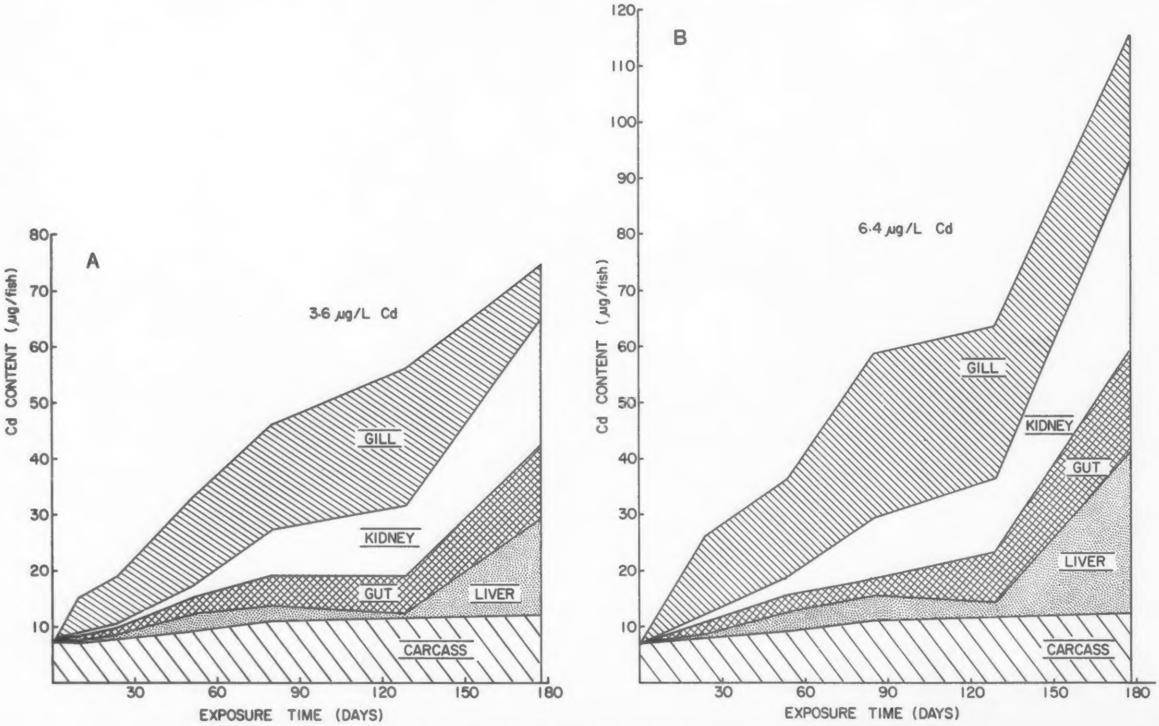

FIG. 6. Change in body burden of cadmium with time in rainbow trout exposed to (A) 3.6 and (B) 6.4 µg Cd/L.

Discussion

The present results demonstrate that although the rates and temporal patterns of cadmium accumulation in various tissues and organs of rainbow trout are widely divergent, the overall result of exposure to dissolved cadmium at concentrations of 3.6 and 6.4 μg/L is a progressive increase in whole-body cadmium burden during a 25-wk period. At the termination of the study, whole-body contents of cadmium were 7- and 11-fold higher in fish exposed to 3.6 and 6.4 μg Cd/L, respectively, than in control fish. A factor that may complicate the interpretation of these results was the increase in temperature during the final 3 wk of exposure. A 5°C increase in water temperature could increase oxygen consumption by 20–33% depending upon the level of swimming activity by the fish (Brett and Glass 1973). If the rate of cadmium accumulation was increased by a similar factor, then the total burden of cadmium accumulated in the last 50-d sampling interval would be elevated by about 10%. Although substantial, this result would not have a significant effect upon the conclusions reached in this study.

Reports on the pattern of cadmium uptake in fish can be divided into two groups based on the presence or absence of a plateau in cadmium accumulation. Plateaus in cadmium accumulation after 2–3 mo have been reported in zebrafish, *Brachydanio rerio*, fed cadmium-contaminated food (Rehwoldt and Karimian-Teherani 1976) and in largemouth bass, *Micropterus salmoides*, and bluegill, *Lepomis macrochirus*, exposed to various levels of dissolved cadmium (Cearley and Coleman 1974). In a major study of cadmium toxicity in three generations of brook trout, *Salvelinus fontinalis*, exposed to 0.5 and 3.4 μg Cd/L, Benoit et al. (1976) observed plateaus in cadmium accumulation by several tissues after 20 wk of exposure. These tissue cadmium levels were maintained for more than 100 wk. The maximum levels of cadmium reported for liver, kidney, and gill of the trout exposed to 3.4 μg Cd/L by Benoit et al. (1976) were approximately 10, 50, and 7 μg/g dry weight, respectively, which are comparable with the respective values of 10 and 21 μg/g observed in liver and kidney but less than the 23 μg/g observed in gill of rainbow trout exposed to 3.6 μg Cd/L in the present study. Williams and Giesy (1978) observed that cadmium accumulation from water ceased between 4 and 6 wk of exposure but subsequently increased in mosquitofish, *Gambusia affinis*, receiving both waterborne and dietary cadmium.

Rainbow trout exposed to 9 μg Cd/L for periods of up to 36 wk (Thomas et al. 1983) progressively accumulated cadmium in their gills, liver, and kidney throughout the entire test period, with each tissue contributing about 20, 20, and 60%, respectively, to the whole-body burden. Unfortunately, the gut and carcass were not analyzed, and as indicated in the present study, these tissues can contribute substantially to body cadmium content. The temporal changes in the relative concentrations of cadmium in gill, liver, and kidney (Thomas et al. 1983) were qualitatively similar to those of the present study. Quantitative differences (up to an order of magnitude less) in the maximum levels of accumulated cadmium in the study of Thomas et al. (1983) compared with our results are probably due to the very hard well water (260–270 mg/L, total hardness) used in their exposures (Roberts et al. 1979). Elevated calcium levels appear to reduce the rate of cadmium accumulation in natural fish populations (McFarlane and Franzin 1980).

In natural populations of northern pike, *Esox lucius*, and white sucker, *Catostomus commersoni*, residing in cadmium-contaminated lakes, a strong, positive correlation exists between age and liver cadmium concentration (Franzin 1984), which suggests that cadmium accumulation may be continuous over the life span of these fish. Furthermore, in the studies where a definite plateau in cadmium accumulation was observed, the control fish exhibited cadmium levels which were about 10-fold higher than those reported in our investigation and the study of Thomas et al. (1983). This may indicate a prior chronic exposure to cadmium in the studies reporting plateaus in cadmium exposure. Prior exposure to various heavy metals including cadmium has been shown to increase both tolerance and resistance to subsequent cadmium exposure in white suckers (Duncan and Klaverkamp 1983). It is possible, therefore, that the differences in the patterns of cadmium accumulation observed in the two groups of studies may reflect differences in exposure history rather than conflicting mechanisms of cadmium accumulation.

In the present study, muscle and skin accumulated only low levels of cadmium (2–4 times control levels), supporting the observations of others (Kumada et al. 1973; Benoit et al. 1976; Sangalang and Freeman 1979; Wilson et al. 1981; Calamari et al. 1982) on several species of freshwater salmonids. Cadmium accumulated most rapidly in the gill, reaching a plateau within 52 d of exposure. Cadmium accumulated rapidly in the liver but accumulation in this organ ceased or was reversed during a 7-wk interval in the middle of the exposure period. This cessation may have reflected a period of increased hepatic activity associated with sexual development, as discussed by Majewski and Giles (1981). Gut cadmium, while increasing slowly in concentration with time, did not exhibit any form of dose dependency in response to increasing dissolved cadmium concentration. The concentration of cadmium in the kidney, however, rose by two orders of magnitude in the experimental period and generally exhibited a dose-dependent relationship with dissolved cadmium concentration. These characteristics would indicate that kidney may be the most appropriate indicator tissue of cadmium intoxication in freshwater trout, a suggestion supported by the low rate of release of cadmium from kidney upon return to noncontaminated water (Kumada et al. 1980).

The final body burdens of 75 and 114 μg Cd/fish in trout exposured to 3.6 and 6.4 μg Cd/L, respectively, represent average whole-body cadmium concentrations of 0.13 and 0.19 μg/g wet weight, respectively. These values are only two- to threefold higher than the average concentrations reported in three species of fish from the Great Lakes (Lucas et al. 1970) and equal to concentrations reported in 6 of 10 warm-water fish species from an industrially contaminated lake containing 17.3 μg dissolved Cd/L (Murphy et al. 1978). Toxic effects on cardiovascular–respiratory function (Majewski and Giles 1981) and electrolyte regulation (Giles 1984) relating to the present study appear to occur predominantly during the initial phases of exposure when the relative rates of cadmium accumulation are maximal. Thus although metal concentrations in tissues may indicate exposure to the contaminant, they may not relate directly to toxic effects experienced by the fish.

It has been suggested, on the basis of high concentrations of cadmium in the kidney, that this organ is a route for excretion of cadmium in fish (Kumada et al. 1973). The present results do not support this suggestion because the maximum amount of cadmium excreted in the urine over 178 d in a fish exposed to 6.4 μg Cd/L would be 2.8 μg or 2.5% of the accumulated cadmium burden. In mammals with cadmium-induced renal damage, significant quantities of cadmium are excreted in association with metallothionein via the urine (Nordberg 1978). In functionally intact kidneys, however, the cadmium and/or cadmium metallothionein complex may be reabsorbed from the glomerular filtrate and thus inhibit renal excretion of the toxicant. Because kidney function, as judged by urinary losses of calcium, magnesium, sodium, potassium, and chloride and the absence of proteinuria, was not impaired by long-term cadmium exposure (Giles 1984), it is unlikely that renal tissue damage was sufficient to permit a significant amount of cadmium excretion in the present studies. In view of the rapid depuration of cadmium from some tissues after cessation of exposure to waterborne cadmium (Kumada et al. 1973, 1980; Muramoto 1980), some route for cadmium excretion must exist in fish. Muramoto (1980) demonstrated that inclusion of tetrasodium ethylenediaminetetraacetate (EDTA), a metal chelator, in the uncontaminated water increased by twofold the rate of depuration of cadmium from gills and viscera of cadmium-contaminated carp which indicates that leaching from the more permeable body surfaces may be a significant route for the elimination of cadmium in fish.

During the first 24 d of treatment, elevated levels of zinc were observed in the urine of trout exposed to 6.4 μg Cd/L but not in trout exposed to 3.6 μg Cd/L. Thereafter, zinc excretion returned to control levels for the remainder of the test period. Using urine production estimates of Giles (1984), the excretion of zinc over the 24-d period by the high-cadmium treatment group was 0.92 μmol/fish in excess of that in control fish. Within this same interval the treated fish accumulated 0.13 μmol of cadmium in the body. Thus, approximately 7 mol of zinc was excreted via urine per 1 mol of cadmium accumulated. A substantial reduction (25–40%) in the zinc content of viscera and gills during chronic exposure to cadmium has been reported for carp, *Cyprinus carpio* (Muramoto 1980), in which 2 and 6 mol of zinc was lost per 1 mol of cadmium accumulated, respectively. In rats, injection of cadmium may result in in vivo displacement of zinc from metallothionein (Leber and Miya 1976) and the zinc is transported in the plasma without attachment to metallothionein or higher molecular weight protein. Klaverkamp and Duncan (1987) have shown that exposure of white suckers to 660 μg Cd/L resulted in a displacement of zinc from the metallothionein fraction to the low molecular weight fraction of liver cytosol. It is highly probable, therefore, that this zinc would be available for excretion via the kidneys. The return of urinary zinc excretion to control levels may then reflect the synthesis of additional metallothionein which could sequester the cadmium continuing to accumulate in the fish.

In the Northern Hemisphere, high concentrations of dissolved cadmium often appear as pulses in the aquatic environment during spring snowmelt and icemelt (Franzin 1984) and may decline substantially as the metal is absorbed by sediments and biota. Although cadmium can be accumulated by fish from water containing very low (<1 μg/L) concentrations of the metal (Calamari et al. 1982), some studies suggest that dietary cadmium may be the most important source of cadmium contamination for fish (Dallinger and Kautzky 1985) in natural ecosystems. In the present study, a maximum of 2.1% of the cadmium present in the diet was absorbed in control fish, assuming that food was the sole source of cadmium in these fish. In fish exposed to 3.6 and 6.4 μg Cd/L, about 6.6 and 4.2%, respectively, of the total body cadmium burden could be derived from dietary sources if dietary cadmium uptake was similar to that of controls. Full understanding of the patterns of cadmium accumulation in fish from contaminated ecosystems will require studies using environmentally realistic cycles of dissolved cadmium in conjunction with identifiable sources of dietary cadmium.

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Dynamics of Age and Size for a Stochastic Population Model

Richard B. Deriso and Ana M. Parma

International Pacific Halibut Commission, P.O. Box 95009, Seattle, WA 98145, USA

Deriso, R. B., and A. M. Parma. 1988. Dynamics of age and size for a stochastic population model. Can. J. Fish. Aquat. Sci. 45: 1054–1068.

We derive a fully stochastic model for the dynamics of age and size in a population. The key to our derivation is that the assumptions made about stochastic growth and survival, in conjunction with some approximations made in the analysis of size-selective fishing mortality, allow us to propagate through time the probability density function of size of individuals in the population by a recursive update of its parameters. The model permits a concise description of the size distribution at age based on mean log-length and variance. The stochastic process is characterized in the model in just a few parameters: two growth coefficients, one variance parameter associated with growth, instantaneous risk of natural mortality, instantaneous risk of fishing mortality, which is a separable function of size-specific selectivity and annual full recuitment fishing mortality, and initial conditions (year-class strength, initial size distribution). Estimation theory is developed for the model, and likelihood equations are derived which provide statistical principles for setting the trade-off between fitting data on length frequency, on total biomass of catch, and on age frequency. The tractability of the model permits a clear description of sampling probability distributions. A number of simpler models, such as catch-age models and delay-difference models, fit within the theoretical framework of our stochastic model.

On présente un modèle entièrement stochastique pour la détermination de la dynamique de l'âge de la taille dans une population, modèle basé sur les hypothèses élaborées sur la croissance et la survie stochastiques et certaines approximations tirées de l'analyse de la mortalité par pêche sélective quant à la taille. Ces hypothèses et approximations permettent de répartir dans le temps la fonction de densité de probabilité de la taille des individus d'une population à l'aide d'une mise à jour récurrente de ces paramètres. Le modèle permet une description concise de la distribution des tailles selon l'âge basée sur la longueur logarithmique moyenne et la variance. Seuls quelques paramètres caractérisent le processus stochastique : deux coefficients de croissance, un paramètre de la variance liée à la croissance, le risque instantané de mortalité naturelle, le risque instantané de mortalité par pêche (qui est une fonction séparable de la sélectivité liée à la taille et du taux annuel de mortalité par pêche au plein recrutement) et les conditions initiales (inportance de la classe annuelle, distribution initiale des tailles). On élabore une théorie de l'estimation pour le modèle et on déduit des équations de la vraisemblance qui servent de principes statistiques pour établir le choix entre l'ajustement des données selon la fréquence des longueurs, la biomasse totale des prises et la fréquence des âges. La flexibilité du modèle permet une description claire des distributions de probabilité de l'échantillonnage. Un certain nombre de modèles plus simples comme le modèle prises-âge et le modèle retard-différence s'accordent avec les limites théoriques du modèle stochastique présenté.

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Models describing the age and size dynamics of a population are complicated immensely by the inclusion of stochastic elements in adult survival and growth. Thus, stochasticity of the population dynamics of adults is usually ignored. Yet we know that survival and growth are chance events and that data on fish contain random sampling effects. Models have been presented separately for random sampling (e.g. Fournier 1983; Macdonald 1987; Quinn et al. 1983), stochastic growth (e.g. Cohen and Fishman 1980; Kirkpatrick 1984; McCaughran and Powell 1977), and stochastic survival (e.g. Chiang 1968; Dupont 1983). When size-selective sources of mortality are present, as is the case for most fisheries, we must bring size into demographic analysis in order to correctly model mortality. Also, resulting patterns of size distribution at age may give a distorted picture of the underlying growth process when interpreted independently of the survival dynamics. The situation worsens when the sampling device (usually the fishery itself) is also size selective (Jones and Mathews 1986). Although these problems have long been recognized (Ricker 1975), a comprehensive fish model which incorporates a stochastic treatment of all the components (growth, survival, and sampling) has not yet been developed, to our knowledge. The main stumbling block as far as we can tell has been the intractability of the probability density functions (pdf) that govern the processes, although Kirkpatrick (1984) was able to solve for the pdf in a size-structured model.

We derive a fully stochastic model for the size and age distribution of a population. The key to our derivation is that the assumptions made about growth and survival allow us to propagate through time the pdf of size of individuals in the population by a recursive update of its parameters. Specifically, we use the result in probability theory that when a Bayesian update of a normal pdf is made with another normal pdf, then the updated pdf is also normal. In the jargon of probability theory, a normal pdf is said to be a "conjugate function" to a normal pdf. The minor variant of this theme that we noticed is that the conjugate function does not need to be normal; indeed the exponential of any second-order polynomial will work, as long as the variance stays positive when updated. We apply this result by approximating size selectivity of fishing mortality with a second-order polynomial, for the range of sizes corresponding to a singe cohort in a given year. A normal density for the logarithm of size of individuals in the cohort will, thus, be updated to a log-normal pdf for size of the survivors.

A major consequence of the assumptions made about growth and survival is that the resultant population model and its pdf's are tractable. Furthermore, the stochastic process is characterized in the model in just a few parameters: two growth coefficients, one variance parameter associated with growth, instantaneous risk of natural mortality, instantaneous risk of fishing mortality, which is a separable function of size-specific selectivity and annual full recuitment fishing mortality, and initial conditions (year-class strength, initial size distribution). We can easily construct configurations of the model with fewer parameters than the catch-age models presented in Deriso et al. (1985) and only four more than the delay-difference models of Deriso (1980). The model can be implemented on a computer much like deterministic abundance models. The stochastic model has the usual recursive equations to describe expected survival of a year-class and, in addition, a pair of recursive equations to describe the pdf for length of individuals in the year-class. Many fisheries analysis methods (such as yield per recruit analysis) have straightforward generalizations to our stochastic model.

We provide a theoretical framework for analyzing different types of fisheries data. The theory is comprehensive enough to allow stock abundance estimation to be made directly from detailed sample data on lengths and (or) age–lengths. Aggregate data (such as total annual catch) can also be used to fit the stochastic model, since the computer can sum up whatever quantities we might want it to. Our suggestion to "let the computer add the numbers" enhances the flexibility of abundance estimation. Novel types of sampling designs are accommodated: for example, age determination of sampled catch could be done every other year for, say, only fish in the small length categories; or we could just classify catch into small, medium, and large sizes. The options are infinite in number. With the theoretical framework given in this paper, "optimal" sampling design takes on a truly comprehensive perspective.

The paper is divided into six main sections. First, we derive the growth model for size. Second, we derive the survival model, which includes the development of a size-selective fishing mortality. Third, we combine the growth and survival models to derive equations which describe the population dynamics of year-classes, as well as the whole population. Fourth, we derive two methods for approximating size selectivity of fishing mortality. Fifth, we develop an estimation theory for the stochastic population model. Sixth, we discuss some generalizations and simplifications of our methods and then relate them to other methods. A glossary of parameters and functions is given in Appendix V. The governing equations for growth and survival of a cohort are listed in Table 1. In Table 2, we list the principal assumptions and approximations made in the derivation of the stochastic population model.

Growth

The size of individuals is usually assumed to follow one of the growth models listed in Fletcher (1975) or Schnute (1981). The basic problem with all those models is that growth rate is deterministic: all individuals of the same size grow at the same rate. In fitting those models to data, however, random errors are usually added to some transformation of predicted size. While this does allow us to consider the model as being stochastic, it is an ad hoc approach for including randomness in the growth process. Cohen and Fishman (1980) took a step away from this conventional approach by showing how annual variability can be included in the von Bertalanffy model. They added a normal random variable (rv) to the difference length equation for individual fish to obtain

$$L_{a+1} = \tilde{\alpha} + \rho L_a + \epsilon$$

where L_a = length of a given fish at age a, $\tilde{\alpha} = L_\infty(1-\rho)$, $\rho = e^{-K}$, discrete Brody growth coefficient, ϵ = normal rv with

TABLE 1. Governing equations for growth and survival of a cohort. The quadratic selectivity function has coefficients which are specific to the age of the cohort. Year indices have been dropped from all notation in the table. Fish size x is the logarithm of length of a fish.

Growth model	$x_{a+1} = \alpha + \beta x_a + \epsilon, \epsilon \sim N(0,V_\epsilon)$
Fishing mortality risk model	$FS(x) = F[b_0 + b_1 x + b_2 x^2]$
Distribution of x in the cohort	$x_a \sim N(E_x(a), V_x(a))$
Recursive equation for E_x	$E_x(a+1) = \alpha + \beta \left[\frac{E_x(a) - b_1 FV_x(a)}{2b_2 FV_x(a)+1}\right]$
Recursive equation for V_s	$V_x(a+1) = \frac{\beta^2 V_x(a)}{2b_2 FV_x(a)+1} + V_\epsilon$
Probability of avoiding capture	$p(a) = \frac{1}{\sqrt{2b_2 FV_x(a)+1}}$
	$\times \exp\left[-Fb_0 - F\left(\frac{b_2 E_x(a)^2 + b_1 E_x(a) - b_1^2 V_x(a) F/2}{2b_2 FV_x(a)+1}\right)\right]$
Probability of annual survival	$l(a+1)/l(a) = e^{-M} p(a)$

TABLE 2. Principal assumptions and approximations made in the development of the stochastic population model.

Principal assumptions

1. The year is divided into two parts, with fishing taking place in one part and growth in the other
2. The pdf of the logarithm of length of the individuals of a cohort at the youngest age of recruitment into the fishery is normal
3. The size-selective risk of fishing mortality is separable into a product of full-recruitment fishing mortality rate F_t and a size-selectivity factor $S(x)$
4. Growth of individual fish is given by equation (1), which is a Gompertz growth model with an additive normal random variable
5. Weight of individual fish is given by an allometric function of length with a multiplicative log-normal random variable
6. Annual survival of a fish of size x is assumed to be probabilistic. The probability of annual survival is $\exp[-FS(x)-M]$, which is composed of size-selective risk of fishing mortality and risk of natural mortality M

Principal approximations

1. Size-selectivity of fishing mortality $S(x)$ is approximated by a quadratic polynomial, which has coefficients specific to each cohort in each year
2. The expected value of the ratio of age-specific abundance to total population abundance in any given year is approximated by the ratio of their respective expected values

mean $E[\epsilon] = 0$ and constant variance V_ϵ, L_∞ = asymptotic length, and K = Brody growth rate parameter.

This model is certainly an improvement over the conventional Bertalanffy model in that the stochasticity in growth is explicitly incorporated. If the initial distribution of size in a cohort is assumed to be a normal distribution, then size, as determined by the model above, will remain normally distributed throughout the lifetime of the cohort (Cohen and Fishman 1980). Distributions of size-at-age, however, usually show some degree of skewness. A simple way of including skewness is to assume a log-normal distribution for size-at-age. This leads us to consider growth in a discrete log-length model:

$$(1)\quad x_{a+1} = \alpha + \beta x_a + \epsilon$$

where $\epsilon \sim N(0,V_\epsilon)$. Here, x_a is the natural logarithm of length of an individual of age a. Later under the Generalizations and Alternatives section of the Discussion, we show that the log-normal assumption can be relaxed to incorporate any arbitrary degree of skewness in the distribution of size-at-age. The model in (1) is a stochastic generalization of the Gompertz growth model applied to length. We can see that by writing the deterministic Gompertz model in its integrated form

$$L_a = L_\infty \exp(-\beta^{a-a_0})$$

and then take logarithms and differences. The parameter L_∞ above is equal to $\exp[\alpha/(1-\beta)]$.

The Gompertz model can be viewed either as an approximation to the Bertalanffy length model or as the appropriate model in its own right. The Gompertz model is a very good approximation ($R^2 > 0.98$ in our own tests) to the Bertalanffy length model for the top 63% of the curve, the 63% number corresponding to the Gompertz inflection point. Since many fisheries catch fish in this size range, the Gompertz model provides a reliable approximation of a Bertalanffy model of growth for exploitable fish.

The stochastic Gompertz model (1) can be written as an age-dependent model by following the procedure described in Cohen and Fishman (1980). Let $a = 0$ denote the initial coded age that we begin modelling a given cohort and assume that x_0, initial log-length of an individual chosen at random, is distributed normally with mean $E_x(0)$ and variance $V_x(0)$. Then *in the absence of size-specific mortality* the log-length distribution of the cohort at age a is normal with mean and variance, respectively,

$$(2)\quad \begin{aligned} E_x(a) &= \frac{\alpha}{1-\beta} + \left[E_x(0) - \frac{\alpha}{1-\beta}\right]\beta^a \\ V_x(a) &= V_x(0)\beta^{2a} + V_\epsilon\,\frac{1-\beta^{2a}}{1-\beta^2} \end{aligned}$$

which is identical to equation (2.9) in Cohen and Fishman (1980), except for the transformation to log-length. We emphasize that equation (2) is valid only when mortality is independent of the size of fish. Fishing gear selectivity will alter the average size of a cohort, as we shall see later in this paper.

Another useful feature of the growth model in (1) is that it is linear as written there. Thus, when $V_\epsilon = 0$ the binomial theorem can be applied to the jth power of log-length x^j_{a+1} and it can be expanded in terms of lower powers of log-length. We have just proved that the size-structured models of Fournier and Doonan (1987) and Schnute (1987) can be generalized to populations where the size distribution of catch is log-normal. One merely replaces length (weight) in their models by log-length (log-weight) and say that the growth model is now a Gompertz model. One disadvantage to this simplification is that we lose the stochastic growth structure specified by (1).

We assume that weight of a fish is related stochastically to length by the power curve

$$W = mL^r e^\nu$$

where $\nu \sim N(0,V_\nu)$. Since log-weight is a linear transformation of log-length, equation (1) can be easily modified to describe the weight dynamics. In the absence of fishing, the pdf for $\ln(W)$ at a given age a is normal with mean and variance, respectively,

$$\begin{aligned} E[\ln(W)] &= \ln(m) + rE_x(a) \\ V[\ln(W)] &= r^2V_x(a) + V_\nu. \end{aligned}$$

The assumption in model (2) that length-at-age is log-normally distributed is supported by data on Pacific halibut (*Hippoglossus stenolepis*). Figure 1 shows the length frequency of 8-yr-old halibut obtained from International Pacific Halibut Commission (IPHC) research cruises in the Pacific Ocean side of Alaska. The second length frequency shown there is an estimate of the population length frequency of 8-yr-olds, which was obtained by dividing research catch by the longline selectivity estimates given in Myhre (1969). The adjusted frequency is probably overcorrected at smaller sizes owing to a change in hook type (to circle) from the "J" hook analyzed in Myhre's paper. Despite this possible overcorrection, it is clear in the Fig. 1 that the length frequency distribution for a cohort is skewed, similar to what occurs with a log-normal distribution. Gear selectivity causes the observed length distribution of catch to differ substantially from the length distribution of the population. McCaughran (1981) provided additional evidence in support of the log-normal distribution for length of halibut.

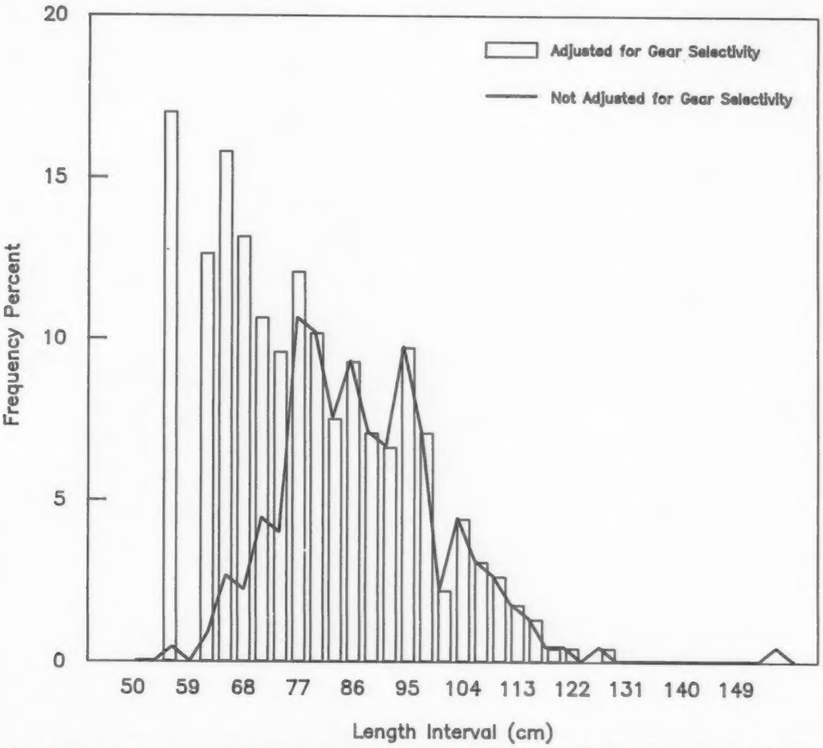

FIG. 1. Length frequency distribution 8-yr-old Pacific halibut collected by longline survey fishing in the Gulf of Alaska in 1985. The original catch distribution is shown with a solid line for 5-cm length categories. The box histogram is catch divided by size selectivity of longline gear (from Myhre 1969).

Survival

Fishing gear is typically selective for specific sizes of fish. In general, gear selectivity curves come in two generic forms: those in which fishing power increases gradually with fish size (perhaps to a maximum power) and then remains high for large fish and those that reach a peak selectivity at some intermediate size. The selection process is size related in both cases. In catch-age analysis we usually approximate what we think is going on — size selection — with an age selectivity factor. In catch-age analysis we go even further and assume that the age selectivity factor is independent of overall fishing effort (Deriso et al. 1985). This allows us to parameterize age-specific fishing mortality in a given year as the product of an age selectivity factor and full recruitment fishing mortality. We follow a similar approach here, but with two significant improvements: we replace age selectivity by size selectivity and we assume that fishing mortality is probabilistic in nature.

We assume that the probability of capture for an individual of size x in year t is given by

$$(3)\quad \text{pr(fish captured}|x) = 1 - e^{-F(t,x)}$$

where $F(t,x)$, size-specific fishing mortality rate for year t, is assumed to be separable into a product of a full-recruitment fishing mortality rate F_t and a selectivity factor $S(x)$, which is only a function of size:

$$(4)\quad F(t,x) = F_t S(x).$$

The fishing mortality rate $F(t,x)$ is proportional to the instantaneous risk of capture (Dupont 1983) and commonly called a *hazard function* in stochastic processes literature. The exploitation model above does not contain natural mortality. This type of approximation is often used in fisheries models (such as Pope 1972).

We structure the sequence of mortality processes in our model so that fishing takes place first followed by natural mortality. The probability that an individual of size x survives the fishery in year t can be written from equations (3) and (4) as

$$(5)\quad \text{pr(fish survives}|x) = e^{-F_t S(x)}$$

where pr(·) denotes probability that event (·) occurs.

In this paper, we assume that the risk of natural mortality is independent of size, and anything else for that matter. The model can be extended to size-dependent natural mortality by employing a procedure analogous to the one given above for size-selective fishing mortality. Let M, the hazard function for natural mortality, be a constant; then $\exp(-M)$ is the probability that an individual does not die from natural mortality over a year. Thus the probability that an individual of size x survives from both fishing and natural mortality for a given year t can be written as

$$\text{pr(annual survival}|x) = e^{-M-F_t S(x)}.$$

Population Dynamics for a Single Year-Class

Growth

We break year t into two parts with fishing occurring in the first part and natural mortality and growth occurring in the second part. Notation conventions in this section are needed to describe normal probability density functions at two times of the year. A complete glossary of parameters and functions is given in Appendix V. The governing equations for growth and survival of a cohort are listed in Table 1. In Table 2, we list the principal assumptions and approximations made in the derivation of the stochastic population model. Let t = beginning of year t, a = age at time t, $t + \tau$ = beginning of the second part of year t, after fishing, $E_x(a,t)$ = mean log-length of a cohort at age a, time t, $V_x(a,t)$ = variance of log-length of the cohort at age a, time t, $\varphi(x|a,t)$ = normal pdf with mean $E_x(a,t)$ and variance $V_x(a,t)$, evaluated at x, and $f(\cdot)$ = general notation for a pdf.

Since harvest is assumed to be size selective, the pdf for log-length of a cohort will be altered over a fishing season. Suppose that x, the logarithm of length of individuals who are age a in year t, has a normal pdf just prior to the fishing season; this is denoted by $\varphi(x|a,t)$. Then, the pdf of x after the fishing season can be written using Bayes theorem as

$$(6)\quad f(x|\text{fish survives}) = \frac{\text{pr(fish survives}|x)\ \varphi(x|a,t)}{\text{Normalizing factor}}$$

where pr(fish survives|x) is the conditional probability of a fish surviving the harvest, given that its log-length is x (equation (5)). The normalizing factor in the denominator of (6) is the integral of the numerator in (6) with respect to x across its entire range from $-\infty$ to ∞. The normalizing factor is therefore the probability that a randomly selected individual in the cohort survives the harvest, as described in the next section of the paper.

As shown in Appendix I, the normality of the distribution of x prior to the fishing season can be preserved in the pdf of x after the harvest by approximating the (arbitrary) size-selectivity function by a quadratic polynomial of x. That is, if

$$(7)\quad \begin{aligned} &S(x) \approx b_0 + b_1x + b_2x^2, \text{ then} \\ &f(x|\text{fish survives}) \approx \varphi(x|a+\tau,t+\tau). \end{aligned}$$

Later in the paper we devote a section to the derivation of two methods for approximating selectivity with quadratic functions.

Figure 2 shows that quadratic polynomials can nicely approximate a sigmoid shaped selectivity funcion, typical of selectivity of longline gear. In general, better estimates of the successive size distributions of a cohort over its lifetime will be achieved by using different quadratic polynomials for each age of a cohort. The overlap in successive approximations of selectivity shown in Fig. 2 corresponds to the overlap in the size ranges of successive age categories. The selectivity curve and size distributions used to construct Fig. 2 correspond roughly to data available on Pacific halibut. The use of "Pacific-halibut-like" parameter values (here and also in later figures) is useful for illustrative purposes; this paper is not meant to present an analysis of Pacific halibut.

In Appendix I, we show that the approximate pdf given in (7) for log-length is normal with mean and variance, respectively,

$$(8)\quad \begin{aligned} E_x(a+\tau,t+\tau) &= \frac{E_x(a,t) - b_1F_tV_x(a,t)}{2b_2F_tV_x(a,t)+1} \\ V_x(a+\tau,t+\tau) &= \frac{V_x(a,t)}{2b_2F_tV_x(a,t)+1}. \end{aligned}$$

The length frequency distribution for the cohort at the beginning of year $t+1$ is obtained by applying growth model (1) to the normal distribution of log-lengths in equation (7). Appendix I

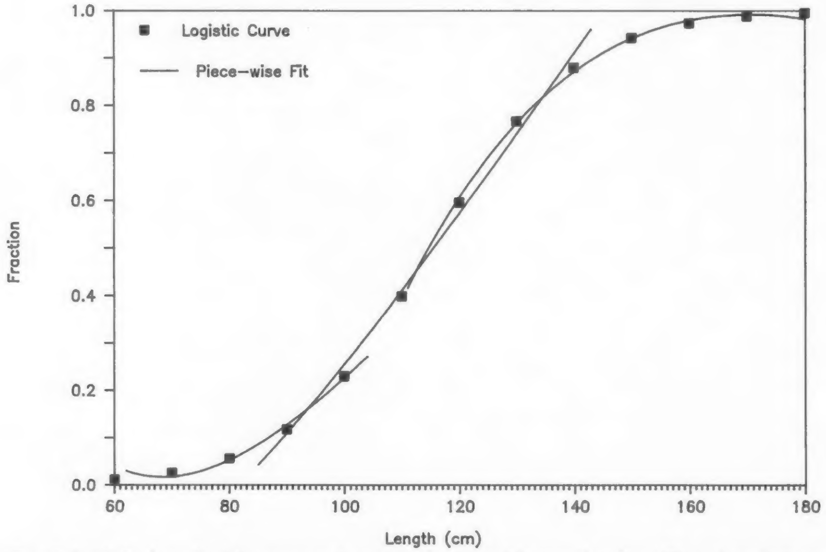

FIG. 2. Logistic size-selectivity curve and a series of polynomial approximations. The polynomials are of second order and were fitted with least-squares to the logistic curve for three fixed size ranges. The size ranges correspond to mean length ± 1.5 SD for fish of mean length 80, 110, and 140 cm. Corresponding error estimates for the approximations are listed in Table 3.

shows that the pdf for log-length of an individual of age $a+1$ selected at random from the cohort is normally distributed. The mean and variance of the log-length distribution can be written as recursive equations:

$$
(9)\quad
\begin{aligned}
E_x(a+1,t+1) &= \alpha+\beta\left[\frac{E_x(a,t)-b_1F_tV_x(a,t)}{2b_2F_tV_x(a,t)+1}\right]\\
V_x(a+1,t+1) &= \frac{\beta^2V_x(a,t)}{2b_2F_tV_x(a,t)+1}+V_\epsilon.
\end{aligned}
$$

Size-selective fishing affects both the mean and the variance of cohort lengths in a nonlinear manner, as we show in (9). Figure 3 illustrates the effect of fishing on the mean and variance of cohort lengths; parameters used for the figure roughly correspond to Pacific halibut. Size-selective fishing mortality causes a selective fishery removal of larger individuals in the cohort, but this affects mean (and median) length only slightly in our example. Fishing has virtually no effect on the confidence bands shown in the Fig. 3, which are defined as four times the standard deviation of length.

Survival and Abundance

The right-hand side of equation (6) can be developed further to get the probability of survival from fishing in year t for an individual selected at random from the population at the beginning of the year. The numerator of equation (6) is the joint density function for survival and log-length. Thus, $p(a,t)$, the probability a randomly selected individual avoids capture, is given by the marginal distribution

$$p(a,t)=\int_{-\infty}^{\infty} e^{-F_tS(x)}\,\varphi(x|a,t)dx.$$

In Appendix I, we evaluate this integral for the approximate selectivity function listed in (7) and obtain

$$
(10)\quad p(a,t)=\frac{1}{\sqrt{2b_2F_tV_x(a,t)+1}}\exp\left\{F_tb_0 - F_t\left(\frac{b_2E_x(a,t)^2+b_1E_x(a,t)-b_1^2V_x(a,t)F_t/2}{2b_2F_tV_x(a,t)+1}\right)\right\}.
$$

Equation (10) looks complicated because $p(a,t)$ results from the interaction of length frequency of the population with a risk of death that depends nonlinearly on size. When the polynomial coefficient b_2 is zero, such as for linear selectivity curves, the formula simplifies considerably to

$$p(a,t) = e^{-F_t(b_0+b_1\bar{x})}$$

where $\bar{x}$ is the average of two means: $\bar{x} = [\mathrm{E}_x(a,t)+E_x(a+\tau,t+\tau)]/2$. Here we see that the probability a randomly selected individual avoids capture in year t equals the probability of surviving fishing for an individual of average length $\bar{x}$. The probability a randomly selected individual survives for the entire year is simply the product of (10) with $\exp(-M)$.

Abundance of the cohort in any given year can be viewed as a particular realization of the stochastic process of survival from age of recruitment to current age. The probability that abundance of the cohort in year t equals $N(a,t)$ given recruitment and past survival probability is binomially distributed:

$$
(11)\quad \mathrm{pr}(N(a,t)|R_{t-a},l(a,t)) = \binom{R_{t-a}}{N(a,t)}\, l(a,t)^{N(a,t)}[1-l(a,t)]^{R_{t-a}-N(a,t)}
$$

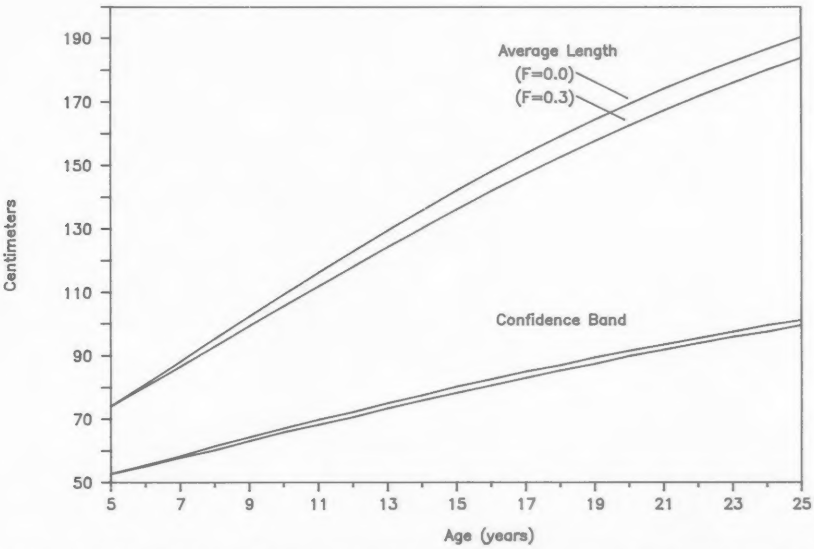

FIG. 3. Average length and confidence band (4 SD) for fish in a population whose dynamics are given by the model in this paper. Calculations were made for an unexploited population ($F = 0.0$) and for an exploited population ($F = 0.3$). The confidence band is slightly lower when $F = 0.3$, but too close to be labelled on the figure. Parameter values correspond roughly to Pacific halibut: $b_0 = -14.0$, $b_1 = 5.5$, $b_2 = -0.5$, $M = 0.2$, $\alpha = 0.42$, $\beta = 0.92$, $V_x(0,t) = 0.031$, $V_\epsilon = 0.0025$, $x_0 = 4.29$. The selectivity curve is a single quadratic polynomial, which corresponds roughly to the selectivity curve given in Myhre (1969).

where $l(a,t) = e^{-Ma} \prod_{j=1} p(a-j,t-j)$, $l(a,t)$ = cumulative probability of survival from reference age 0 to age a, and R_{t-a} = abundance of reference age 0 fish in year $t-a$. Reference age 0 should be chosen to reflect size of fish in a cohort before many of them become vulnerable to fishing. The mean and variance of cohort abundance is given, respectively, by

$$E_N(a,t) = R_{t-a}l(a,t)$$
$$V_N(a,t) = R_{t-a}l(a,t)[1-l(a,t)].$$

One subtlety of our stochastic model is that the $l(a,t)$ probabilities are actually conditional probabilities. They depend on the size distribution of the cohort through the size-dependent risk of fishing mortality. The equation written in (11) then is conditional on the growth parameters for the cohort, past F_t, as well as mean log-length for recruits and its variance.

Catch

The pdf for log-length of the catch from a cohort is the complement of the pdf in (6):

$$f^c(x|a,t) = \frac{(1-e^{-F_tS(x)})\varphi(x|a,t)}{\text{Normalizing factor}}$$

where $f^c(x|a,t)$ is defined to be the pdf for log-length of a fish chosen randomly from catch of the cohort of age a in year t. The normalizing factor above is the integral of the numerator with respect to x across its entire range; thus, the normalizing factor is $[1-p(a,t)]$, as shown in Appendix I. The pdf of length in the catch depends on fishing mortality. As shown in Appendix I, the density function $f^c(x|a,t)$ can be written as a linear combination of two normal density functions:

$$(12)\quad f^c(x|a,t) = \frac{\varphi(x|a,t) - p(a,t)\varphi(x|a+\tau,t+\tau)}{1-p(a,t)}.$$

The pdf above is not a normal density function, nor would we expect it to be even approximately normal, since size-selective fishing mortality induces a skew in the size-at-age distribution in the catch. However, the pdf in (12) is a simple function of x and, thus, amenable to many types of estimation or forecasting we might want to try. The moments of (12) are just a linear combination of the moments of its normal components. Therefore, we can find exact expressions for the mean and variance. Let $m_2^c(a,t)$ denote the second moment; then we can write the mean, second moment, and variance for the distribution of log-lengths in the catch of the cohort, respectively, as

$$E_x^c(a,t) = \frac{E_x(a,t) - p(a,t)\,E_x(a+\tau,t+\tau)}{1-p(a,t)}$$

$$(13)\quad m_2^c(a,t) =$$
$$\frac{[V_x(a,t)+E_x(a,t)^2] - p(a,t)[V_x(a+\tau,t+\tau)+E_x(a+\tau,t+\tau)^2]}{1-p(a,t)}$$

$$V_x^c(a,t) = m_2^c(a,t) - E_x^c(a,t)^2.$$

Mean log-length of a given cohort in the catch is biased in comparison with mean log-length in the population. We can see this most easily when selectivity is a linear function of x, that is $b_2 = 0$. Here we can simplify the formula for expected log-length of the catch, as given in (13), to obtain

$$E_x^c(a,t) = E_x(a,t) + \frac{b_1p(a,t)F_tV_x(a,t)}{1-p(a,t)}.$$

The bias between log-length in the population versus log-length in the catch is given by the difference $E_x(a,t) - E_x^c(a,t)$. The bias terms simplify further when fishing mortality is very small, $F_t \approx 0$, such as in survey catch. In this case, we substitute the value 1 for $p(a,t)$ in the numerator above and $F_tS(\bar{x})$ for $1-p(a,t)$ in the denominator to get

$$E_x(a,t) - E_x^c(a,t) \approx \frac{-b_1V_x(a,t)}{S(\bar{x})}$$

where $\bar{x}$ is the average of two means: $[E_x(a,t)+E_x(a+\tau,t+\tau)]/2$. The bias, in the linear selectivity case, then depends jointly on the slope of the selectivity curve b_1, the variance of log-length, and selectivity of an individual of size $\bar{x}$. Jones and Mathews (1986) derived a similar formula for bias of length in the catch. They presented a numerical example in which the bias in the estimate of K, obtained from a Ford–Walford plot of catch size-at-age data, is small (3%) when the following conditions are satisfied: a small bias occurs between mean length in the catch and length in the population, the bias in length is a constant value for successive age categories, and L_∞ is a known value.

Number of individuals in the catch depends stochastically on the abundance of the cohort and the probability of capture. The probability that catch of the cohort in year t equals $C(a,t)$ given $N(a,t)$ and $p(a,t)$ is, therefore, binomially distributed with mean and variance, respectively,

$$(14)\quad \begin{aligned} E_N^c(a,t) &= N(a,t)[1-p(a,t)] \\ V_N^c(a,t) &= N(a,t)[1-p(a,t)]p(a,t). \end{aligned}$$

The probability parameter $p(a,t)$ in (14) depends on the size distribution of the cohort because of the size-dependent risk of fishing mortality.

Size Distributions for Aggregated Ages

Length frequency for the total population can be written down directly now that the dynamics of year-classes are known. In a given year t, the pdf for log-length of a fish chosen randomly from the population is given by the marginal distribution

$$(15)\quad f(x|t) = \sum_{a=0}^{A} \varphi(x|a,t)\,P_{a,t}$$

where $P_{a,t}$ is the probability that an individual selected at random from the population in year t is of age a. In Appendix II, we show that $P_{a,t}$ is approximately expected abundance of the a-yr-old divided by total expected abundance:

$$P_{a,t} = \frac{E_N(a,t)}{E_N(t)}$$

to an accuracy of order $o(1/E_N(t))$, where $E_N(t) = \Sigma_{i=0}^{A} E_N(i,t)$ is total expected abundance. Moments for the log-length density above are linear combinations of moments for its component normal densities. Therefore, mean log-length of the population, second moment m_2, and variance are given by

$$E_x(t) = \sum_{a=0}^{A} E_x(a,t)P_{a,t},$$

$$m_2 = \sum_{a=0}^{A} [V_x(a,t)+E_x(a,t)^2]\,P_{a,t},$$

$$V_x(t) = m_2 - E_x(t)^2.$$

Weight frequency for the total population is similar to length under the logarithmic transformation. Since we assume a stochastic allometric weight–length relationship, shown after (2), log-weight is linearly related to log-length by $\ln(W) = \ln(m) + rx + v$. Therefore, we can write down the mean and variance of log-weight for the total population as

$$\begin{aligned} \text{Mean} &= \ln(m) + rE_x(t) \\ \text{Variance} &= r^2 V_x(t) + V_v. \end{aligned}$$

Length frequency for total catch in a given year is based on a derivation similar to the one above in (15). Weight frequency of the catch is shown in Appendix III. In a given year t, the pdf for log-length of a fish chosen randomly from the catch is given by

$$(16) \quad f^c(x|t) = \sum_{a=0}^{A} f^c(x|a,t)\, P^c_{a,t}$$

where $P^c_{a,t}$ is the probability that an individual selected at random from the catch in year t is of age a. In Appendix II, we show that $P^c_{a,t}$ is approximately the ratio of expected catch of the a-yr-olds divided by total expected catch:

$$P^c_{a,t} = \frac{[1 - p(a,t)]E_N(a,t)}{\Sigma^A_{a=0}[1 - p(a,t)]E_N(a,t)}$$

to an accuracy of order $o(1/(\text{total expected catch}))$. Moments for the log-length of catch are linear combinations of moments for its component normal densities. Therefore, mean log-length of the catch, second moment m^c_2, and variance are given by

$$E^c_x(t) = \sum_{a=0}^{A} E^c_x(a,t)\, P^c_{a,t},$$

$$m^c_2 = \sum_{a=0}^{A} m^c_2(a,t)\, P^c_{a,t}$$

$$V^c_x(t) = m^c_2 - E^c_x(t)^2.$$

Figure 4 shows the stationary probability distribution of size in the catch and in the population for fish of three fixed ages. The joint pdf functions used to construct the Fig. 4 are the age-specific terms from the right-hand side of equations (15) and (16). Parameter values chosen for the Fig. 4 correspond roughly to female Pacific halibut fished with gear which has a selectivity similar to that given in Myhre (1969). Size-dependent fishing mortality causes the distribution of sizes to differ substantially between the catch and the population. Becuse of the size-dependent mortality, the length frequency, for a given age, becomes less skewed as the fish become older. The pdfs for the age 11 fish look normally distributed, and since these fish are almost fully vulnerable to fishing, the pdf in the catch and in the population are similar in shape and location.

Approximating the Selectivity Function

A result of replacing the "true" selectivity $S(x)$ by a quadratic function is that the normal posterior pdf, $\varphi(x|\text{fish survives})$, is only an approximation of the "true" $f(x|\text{fish survives})$. As a consequence, alternative methods for approximating the selectivity function should be evaluated by computing some measure of distance between the "true" posterior pdf and a given normal approximation. In the analysis that follows, we assumed that the pdf of x prior to the harvest was normal, therefore neglecting the compounding effects of errors introducted at successive fishing seasons. The extent to which the propagation of errors in the model may further deteriorate the performance of the approximation or, to the contrary, some compensation may take place, exceeds the scope of this analysis.

A well-established way to measure the degree of dissimilarity between two pdf is the Kullback's cross-entropy functional, also referred to as the Kullback–Leibler information number (Bickel and Doksum 1977). Here we apply this functional to measure the distance between the "true" and approximated posterior pdf, as given by

$$(17) \quad I[f,\varphi] = \int_{-\infty}^{\infty} \ln\left[\frac{f(x|\text{fish survives})}{\varphi(x|\text{fish survives})}\right] f(x|\text{fish survives})\,dx$$

where $f(x|\text{fish survives})$ is the posterior pdf of x given by equa-

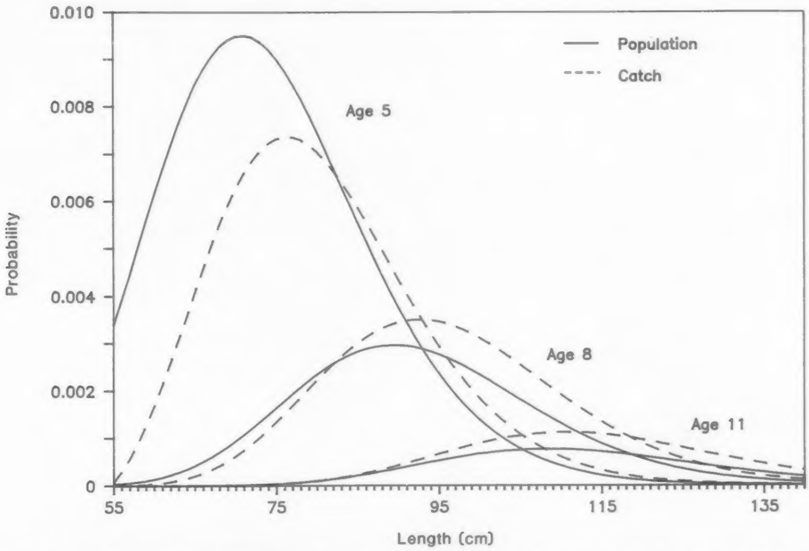

FIG. 4. Probability that a fish chosen at random from the population (or catch) will be of length (in 1-cm increments) and age listed. The probabilities shown correspond to the stationary pdf of fish whose dynamics have the parameter values listed in Fig. 3 with $F = 0.3$.

TABLE 3. Mean and variance of logarithm of length x following size-selective harvest, and probability of survival $p(a,t)$ computed using a "true" logistic selectivity (upper figures) and a quadratic approximation of the selectivity function (lower figures) for three mean length values prior to fishing. The selectivity function, together with the quadratic approximations for the three length values, is shown in Fig. 2. Each quadratic approximation is based on at least-squares regression of a quadratic polynomial to the logistic selectivity curve at length values (the squares) indicated on Fig. 2 for each size group. Variance of x prior to fishing is 0.031, and fishing mortality at full selectivity is $F = 0.30$.

	Prior mean length (cm)		
	80	110	140
Posterior mean of x	4.3618 4.3627	4.6712 4.6695	4.9145 4.9130
Posterior variance of x	0.0303 0.0302	0.0304 0.0302	0.0320 0.0329
Survival	0.9737 0.9736	0.8851 0.8838	0.7950 0.8002

tion (6) and $\varphi(x|\text{fish survives})$ is its normal approximation. For continuous functions, it can be shown (see Bickel and Doksum 1977) that $I[f,\varphi]$ is larger or equal to zero, with equality holding if and only if $f(x|\text{fish survives}) = \varphi(x|\text{fish survives})$ for all $x \in (-\infty,\infty)$.

First, we derive a procedure for approximating the selectivity function $S(x)$, for an arbitrary normal prior $\varphi(x)$ representing the pdf of x for individuals of a given age and year. For the purpose of clarity, indices for year and age have been dropped from the notation all throughout this section. Following the criterium above, the best procedure for choosing the polynomial coefficients is that which minimizes $I[f,\varphi]$. In Appendix III we show that $I[f,\varphi]$ is minimized when the following necessary and sufficient conditions are satisfied:

$$\int_{-\infty}^{\infty} x\varphi(x|\text{fish survives})dx = \int_{-\infty}^{\infty} xf(x|\text{fish survives})dx$$

$$\int_{-\infty}^{\infty} x^2\varphi(x|\text{fish survives})dx = \int_{-\infty}^{\infty} x^2f(x|\text{fish survives})dx.$$

These conditions imply that the polynomial coefficients b_1 and b_2 should be such that the mean and variance of x for the approximated and "true" posterior distributions match. Once b_1 and b_2 have been chosen, the b_0 coefficient can be selected so that the unconditional probabilities of survival correspondent to the "true" and approximated functions coincide. This presupposes an additional condition, namely:

$$\int_{-\infty}^{\infty} e^{-F(b_0+b_1x+b_2x^2)}\,\varphi(x)dx = \int_{-\infty}^{\infty} e^{-FS(x)}\,\varphi(x)dx.$$

The implementation of this procedure on a computer program requires the numerical evaluation of the integrals above. The polynomial coefficients are then a function of the first two moments of the posterior distribution of x and the unconditional probability of survival p, although their (b_0, b_1, b_2) computation is no longer required. Solving equations (8) and (10) simultaneously for the three coefficients, we obtain (using now the full notation)

$$F_tb_0 = \ln\left(\frac{1}{p(a,t)}\right) + \frac{1}{2}\ln\left(\frac{V_x(a+\tau,t+\tau)}{V_x(a,t)}\right) - \frac{1}{2}\left[\frac{E_x(a,t)^2}{V_x(a,t)} - \frac{E_x(a+\tau,t+\tau)^2}{V_x(a+\tau,t+\tau)}\right]$$

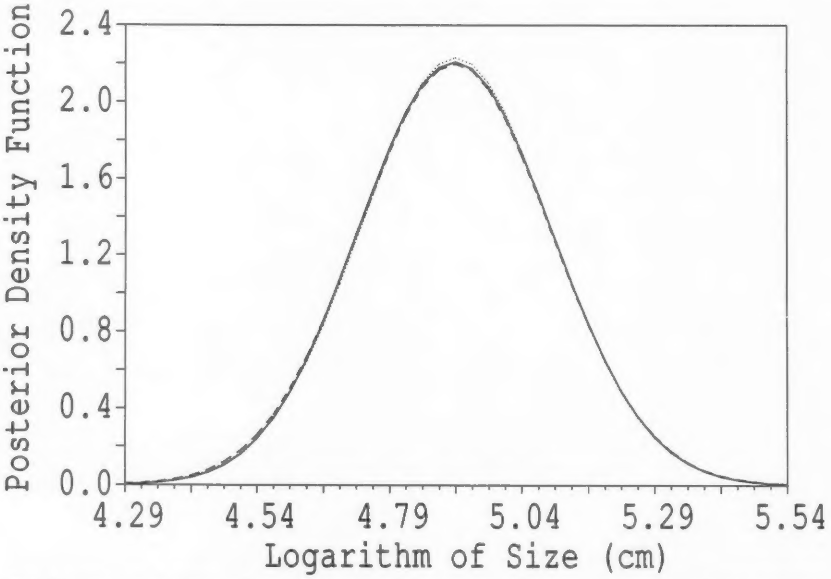

FIG. 5. Comparison of two methods of approximating the size distribution of a cohort after size-selective harvest for fish of mean log-length 4.93 and variance 0.031. The closeness of the approximations to the true curve makes it difficult to see labels. The true curve is the solid line, the dotted line is the approximation based on minimizing cross-entropy (equation(17)), and the broken line is the approximation based on least-squares regression of a quadratic polynomial to the true selectivity function. Full-recuitment fishing mortality is set to $F = 0.3$.

$$b_1 = \frac{E_x(a,t)}{F_t V_x(a,t)} - \frac{E_x(a+\tau,t+\tau)}{F_t V_x(a+\tau,t+\tau)}$$

$$b_2 = \frac{1}{2F_t}\left[\frac{1}{V_x(a+\tau,t+\tau)} - \frac{1}{V_x(a,\mathrm{t})}\right]$$

where the mean and variance of x after the harvest, those with $(+\tau)$, were evaluated with the "true" posterior pdf.

An alternative procedure to the cross-entropy minimization is to simply fit a quadratic function to $S(x)$ with linear regression, for a certain range of x values (say from x_l to x_u) around the mean of the prior distribution. This is equivalent to minimizing the squared-error distance:

$$\sum_{x_l}^{x_u} [\ln[e^{-FS(x)}\varphi(x)] - \ln[e^{-F(b_0+b_1x+b_2x^2)}\varphi(x)]]^2 \, \Delta x,$$

that is, the square of the difference between the natural logarithms of the "true" and the approximated functions for the joint probability of surviving the harvest and being of log-length x, summed across $x_l < x < x_u$. This method was used to obtain the approximations to the logistic size-selectivity function shown in Fig. 2. This procedure is computationally efficient, although it does not have the desirable property of assuring a perfect match of the first two moments of x and the unconditional probability of survival. The extent of these problems were explored by evaluating the departures of the posterior mean and variance of x, and the unconditional survival probability obtained by this procedure from the "true" parameters. As shown in Table 3, departures were insignificant when the set of parameters used to construct Fig. 2 was explored.

Figure 5 shows that the posterior pdf's approximated by the two procedures are both visually indistinguishable from the "true" posterior pdf for the worst case of the three in Table 3. Numerical analyses with a wide range of parameter values showed that errors were in general small (less than 5% in our tests, for realistic parameter values). For any given method, the performance of the approximation should vary with the shape of the selectivity curve, the mean and variance of x prior to fishing, and the full-recruitment fishing mortality, F. Intuitively, one can expect that the lower the variance of x, the better the performance of the approximation. In other words, the narrower the range of x values represented in a year-class, the better a quadratic function can fit the true selectivity over that range. With respect to the shape of the selectivity function, an extreme case is knife-edge size selectivity, which clearly would not preserve the normality of a prior distribution of x. In general, one would expect that a steep selectivity curve will not be well approximated over some ranges of x values. Finally, the higher the level of F, the more important the size-selectivity effect and, consequently, the larger the errors introduced in the approximation.

Estimation Theory

A Single Year of Data

The sampling program at IPHC is typical of many fisheries agencies. There are three basic components to our catch sampling (Quinn et al. 1983):

(1) A random sample of the catch is measured for size. Otolith length is measured for Pacific halibut.

(2) A stratified random subsample of the measured fish are aged. Measured halibut are stratified into 5-cm length categories and a random sample is taken from each strata and aged.

(3) The total biomass of the catch is recorded.

Maximum likelihood (ML) estimates of model parameters can be made from all the sampling data. We first present results for the ideal case where there are no ageing errors. In Appendix III, we show that Λ_t, the logarithm of the likelihood function for all data, can be written as a sum of the three sampling components given, up to additive constants, by

$$(18) \quad \Lambda_t = \sum_{i=1}^{NS} \ln[f^c(x_i|t)] \text{ for the first component}$$
$$+ \sum_{j=1}^{NA} \ln[f^c(x_j|a_j,t)P^c_{a_j,t}] \text{ for the second component}$$
$$+ \ln[\varphi(Y_t|E_Y(t),V_Y(t))] \text{ for the third component}$$

where x_i = log-length of the ith sampled fish, which was not aged, (x_j,a_j) = age and log-length of subsampled fish, NS = number of fish measured, but not aged, NA = number of fish measured and aged, and Y_t = biomass of total catch in year t.

The densities in the first and second components are exact. The normal density for the third component should be very accurate as well, owing to the Central Limit Theorem. The mean and variance in the third component are exact, but too lengthy to be listed here (see Appendix IV).

When there are ageing errors, then the second component of the log-likelihood function needs to be changed. We generalize the second component of (18) with a misclassification matrix. Let $\theta(i,a)$ be the probability that a fish of true age i is said to be age a. The second component in (18) is changed to

$$(19) \quad \sum_{j=1}^{NA} \ln\left[\sum_{i=0}^{A} \theta(i,a_j)\, f^c(x_j|i,t)P^c_{i,t}\right]$$

while the rest of Λ_t is the same as given in (18).

Multiple Years of Data

We propose to approximate Λ, the joint log-likelihood of several years of data, by summing Λ_t, a single year log-likelihood, across the T years of data being analyzed. Parameter estimates for growth, abundance, and mortality can be obtained by maximizing

$$(20) \quad \Lambda = \sum_{t=1}^{T} \Lambda_t.$$

The objective function in (20) is approximate because it neglects covariance terms arising from the kernels of the various marginal distributions that make up Λ_t. For example, Dupont (1983) showed that when catch by age and year is perfectly known, then the joint likelihood of the catch data is multinomial, not the product of independent binomials as used in the derivation of (18). Unfortunately, fisheries agencies do not know the catch by age and year perfectly and so we do not make Dupont's assumption. Instead, we assume that sample data give us bits and pieces of information about the age and size structure of the catch. This forces us to work with marginal distributions in most of our theory. A nice feature of marginal distributions is that they integrate out a lot of the covariance. As a consequence, multinomial covariance effects are less in equation (20) than in Dupont's model.

We will probably want to add auxiliary information to the likelihood criteria as well. We can add to Λ the auxiliary sum of squares for fishing effort and sum of squares for a spawner–recruit relationship as given in Deriso et al. (1985).

Discussion

Generalizations and Alternatives

The growth model (1) given in this paper can be used to describe a family of growth curves. By letting x_a be another transformation of length, we get another growth curve. By introducing one more parameter into our model, say λ, we can define a family of growth models by the power transformation of length $x = (L^{\lambda} - 1)/\lambda$ which has the Bertalanffy model ($\lambda = 1$) and Gompertz model ($\lambda \longrightarrow 0$) as special case solutions. The advantage of this more general approach is that the parameter λ defines the shape of the pdf's for length. Carroll and Ruppert (1984) showed that the power transformation can be used to decide between pdf's when fitting certain theoretical models to data.

An alternative to the growth model (1), or its extended family of growth curves described above, is a model with a different assumption about stochasticity in fish growth. As given in (1), the variance of the stochastic term ϵ is independent of x and, more importantly, it is independent of incremental growth $x_{a+1} - x_a$. An alternative assumption about V_ϵ is to assume that it is proportional to expected incremental growth; that is, $V_\epsilon \propto [\alpha + (\beta - 1)E_x(a)]$. This alternative has the property that the variance in growth goes to zero when there is no growth, such as for fish near their asymptotic size.

The fishing mortality model (3) can be generalized in two important ways. First we can make $S(x)$ selectivity depend on age as well as size, since application of the polynomial approximation for $S(x)$ is made in (7) separately for each age (and year) category. This generalization is useful for analysis of fishes, such Atlantic menhaden (*Brevoortia tyrannus*), in which cohorts are spatially segregated when young, irrespective of size.

Multigear fisheries models are similar to the single-gear prototype given earlier. There will be a selectivity curve and a fishing mortality parameter $F_{j,t}$ for the *j*th gear type. Each gear selectivity curve will be approximated by a (year- and age-specific) second-order polynomial. The survival equations and pdf's for length in the population stay the same, except that in the formulae we replace the product of F_t with any given polynomial coefficient by the sum, over gear types, of the product of $F_{j,t}$ and corresponding polynomial coefficient for the *j*th gear. The catch length pdf's are specific for each gear type and must be derived separately from the gear-specific complement to equation (6). A multigear approach is a natural way to bring survey data into the analysis: survey fishing can be viewed as a special gear type in the fishery.

Perhaps the most restrictive assumption in the model is that fish growth must follow the stochastic growth model (1). Genetic variability alone causes us to question that assumption. Size phenotypes are common in most animal broods, there typically being a runt of the litter who stays smaller than siblings throughout its life. Between-sexes heterogeneity in growth is common to many fish species, the Pacific halibut among them (Deriso and Quinn 1983). The selective fishing of faster growing females has a direct consequence on the size of the spawning stock. Our current research is directed towards generalizing the stochastic population model presented here to account for individual variation in parameters of growth, along the lines suggested by Sainsbury (1980) and Cohen and Fishman (1980).

Simplifications

The population model in this paper encompasses many of the population models of fisheries science. The deterministic versions of the equations used here for growth and survival are standard in fisheries analysis. Even the more recent works on size-structured models in Schnute (1987) have a direct analog in our model: set all our equations to deterministic, except for the initial distribution of length for a cohort, and set selectivity to a sigmoid shaped curve to get a model similar to Schnute's. We can derive a population model similar to the one in Fournier and Doonan (1987) by using age selectivity of fishing mortality. We find it difficult to parameterize our model like their catch model where length by age of fish in the catch has a variance which is independent of age.

Catch-age analysis is based on the assumption that total catch can be stratified by age. Our model can be reduced to a catch-age model by altering our estimation scheme. The procedure given in Quinn et al. (1983) for estimating catch-at-age can be used, and predicted catch-at-age from our model can be fitted to the data. A disadvantage of such an approach is that we loose the likelihood formalism of this paper and its statistical principles for setting the trade-off between fitting length frequency, age of subsamples, and total biomass of catch. On the other hand, the stochastic population model derived in this paper can be used to examine the robustness of simpler schemes of parameter estimation.

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Appendix I. Derivations for Population Dynamics for a Single Year-Class

In this appendix, we derive the probability of survival from fishing, and mean and variance formulas for log-length of a cohort, when selectivity is assumed to be a quadratic polynomial, that is,

$$S(x) = b_0 + b_1x + b_2x^2,$$

which can be substituted into equation (5) to give

$$\text{pr(fish survives fishery}|x) = e^{-F_t(b_0+b_1x+b_2x^2)}.$$

We assume that the pdf of size x prior to the start of fishing is normal with mean $E_x(a,t)$ and variance $V_x(a,t)$. Therefore, equation (6) can be rewritten as

$$\text{(I.1)}\quad f(x|\text{fish survives}) =$$

$$\frac{\exp\left\{-F_t(b_0+b_1x+b_2x^2) - \frac{(x-E_x(a,t))^2}{2V_x(a,t)}\right\}}{\sqrt{2\pi V_x(a,t)}\ \text{normalizing factor}}.$$

We write down the terms in the exponential and then expand the terms involving x to get

$$-\left[\frac{2b_2F_tV_x(a,t)+1}{2V_x(a,t)}\right]x^2 + \left[-b_1F_t + \frac{E_x(a,t)}{V_x(a,t)}\right]x.$$

Now, completing the squares of terms in x, we see after some algebra that the pdf for log-length of surviving fish has to be a normal with

$$E_x(a+\tau,t+\tau) = \frac{E_x(a,t) - b_1F_tV_x(a,t)}{2b_2F_tV_x(a,t)+1}$$

$$V_x(a+\tau,t+\tau) = \frac{V_x(a,t)}{2b_2F_tV_x(a,t)+1}.$$

These equations are given in (8) in the text.

In order to get the pdf for $x_{a+1,t+1}$, we apply model (1) to $x_{a+\tau,t+\tau}$. Since (1) is linear on x, and we have shown that $x_{a+\tau,t+\tau} \sim N(E_x(a+\tau,t+\tau),\ V_x(a+t,t+\tau))$, it follows that $x_{a+1,t+1}$ is also normally distributed with

$$E_x(a+1,t+1) = \alpha + \beta E_x(a+\tau,t+\tau)$$
$$V_x(a+1,t+1) = \beta^2V_x(a+\tau,t+\tau) + V_\epsilon,$$

which, after substitution, gives (9) in the text.

The probability, $p(a,t)$, that a randomly selected individual avoids capture is derived by integrating the right-hand side of (I.1), except for the normalizing factor, across x. First, we rewrite that expression as

$$\exp\left\{-F_tb_0 - \left(b_2F_t + \frac{1}{2V_x(a,t)}\right)\right.$$
$$\left.\times\left(\frac{E_x(a,t)^2}{2b_2F_tV_x(a,t)+1} - E_x(a+\tau,t+\tau)^2\right)\right\}$$
$$\times\sqrt{\frac{V_x(a+\tau,t+\tau)}{V_x(a,t)}}\quad\varphi\,(x|a+\tau,t+\tau).$$

Now, the normal pdf cancels in the integration, and equation (10) follows after simplification of the remaining factor. Note that $p(a,t)$ is nothing more than the normalizing factor in (I.1), and thus, the integral of the pdf (I.1) over the range of possible values of x equals 1.

The pdf for log-length by age of fish in the catch $f^c(x|a,t)$ is the complement of the pdf in (I.1), as explained in the text. That is,

$$\text{(I.2)}\quad f^c(x|a,t) = \frac{\varphi(x|a,t) - e^{-F_tS(x)}\varphi(x|a,t)}{\text{Normalizing factor}}.$$

By integrating as before, we see that the normalizing factor in this equation equals $1 - p(a,t)$. The second term in the numerator of (I.2) is the same as the right-hand side of (I.1), excluding the normalizing factor in (I.1); therefore, this second term, as shown above, equals $p(a,t)\varphi(x|a+\tau,t+\tau)$. This leads directly to equation (12).

Appendix II. Derivations for Length Distributions for Aggregated Ages

The probability that an individual selected at random from the population in year t is of age a, conditional on a given vector of population abundance by age, is equal to

$$\text{(II.1)}\quad \frac{N(a,t)}{\Sigma_{i=0}^{A}N(i,t)}.$$

The unconditional probability $P_{a,t}$ is then the marginal of the product of (II.1) and the joint probability of the vector of $N(i,t)$, $i \in [0,A]$:

$$P_{a,t} = \sum_{N(0,t)}\cdots\sum_{N(A,t)}\frac{N(a,t)}{\Sigma_{i=0}^{A}N(i,t)}\prod_{i=0}^{A}\text{pr}(N(i,t)|R_{t-i},l(i,t)),$$

which, by definition of expected value, is

$$P_{a,t} = E[N(a,t)/N(t)]$$

where $N(t)$ is defined to be total abundance $\Sigma_{i=0}^{A}N(i,t)$. Application of the delta method (Seber 1973, p. 7) to $E[N(a,t)/N(t)]$

gives an approximation for the expected value of a ratio which is the ratio of expected values plus a remainder term:

$$P_{a,t} = \frac{E_N(a,t)}{E_N(t)} + R$$

where the remainder is approximated in the delta method as

$$\text{(II.2)}\ R \simeq \left[\sum_{i=0}^{A} \frac{E_N(i,t)E_N(a,t)[1-l(i,t)]}{E_N(t)^3} \right] - \frac{E_N(a,t)[1-l(a,t)]}{E_N(t)^2}$$

and where we define $E_N(t) = \Sigma_{i=0}^{A} E_N(i,t)$. In the application of the delta method, we were required to compute some partial derivatives, and some variances and covariances, which we list below to help the reader reconstruct our derivations:

$$\frac{\partial^2 P_{a,t}}{\partial N_{i,t}^2} = 2N(a,t)/[N(t)^3] \text{ for } i \neq a$$

$$\frac{\partial^2 P_{a,t}}{\partial N_{i,t}^2} = 2N(a,t)/[N(t)^3] - 2/[N(t)^2] \text{ for } i = a$$

$$V_N(i,t) = E_N(i,t)[1-l(i,t)]$$

$$\text{COV}[N(i,t), N(j,t)] = 0 \text{ for } i \neq j.$$

We can now show that

$$\text{(II.3)}\quad -\frac{E_N(a,t)(1-l(a,t))}{E_N(t)^2} < R < \frac{E_N(a,t)l(a,t)}{E_N(t)^2},$$

which implies that $|R|$ is less than $(1/E_N(t))$. First, we rewrite the expression for R in (II.2) as

$$\text{(II.4)}\quad R \simeq -\frac{E_N(a,t)}{E_N(t)^3} \left[\sum_{i=0}^{A} E_N(i,t)l(i,t) \right] + \frac{E_N(a,t)l(a,t)}{E_N(t)^2}$$

and note that R is less than the positive term on the right-hand side of (II.4), which forms the upper bound shown in (II.3). The remaining (negative) term in (II.4) is larger than a similar expression with $l(i,t) = 1$, for $i \in [0,A]$, that is, it is larger than $-E_N(a,t)/E_N(t)^2$, which can be summed to the second (positive) term in (II.4) to give the lower bound in (II.3).

Similarly, $P_{a,t}^c$, the probability that an individual selected at random from the catch in year t is of age a, equals the expected value of the catch by age divided by the total catch. This will be approximated following the approach given above:

$$P_{a,t}^c = \frac{[1-p(a,t)]E_N(a,t)}{\Sigma_{i=0}^{A} [1-p(i,t)]E_N(i,t)}.$$

The derivation is also based on the delta method.

Appendix III. Derivations for Approximating the Selectivity Function

Here we derive a procedure for choosing the coefficients of the quadratic polynomial used to approximate an arbitrary selectivity function. Year indices will be dropped from all notation in this appendix.

As explained in the text, the polynomial coefficients are selected so as to minimize the distance between the "true" and approximated posterior pdf of x, as measured by the Kullback's cross-entropy functional, $I[f,\varphi]$, and the difference between the "true" and approximated survival probabilities. The approximated posterior is actually independent of the b_0 coefficient; when the "true" selectivity is replaced in equation (6) by its quadratic approximation, the factors $\exp\{-Fb_0\}$ in the numerator and denominator cancel out. Equations (8) in the text show that, in fact, the approximated posterior mean and variance of x are independent of b_0. It is the approximated probability of survival, given by

$$\bar{p}(a) = \int_{-\infty}^{\infty} e^{-F(b_0+b_1x+b_2x^2)} \varphi(x|a)dx,$$

that is a function of the three coefficients. Accordingly, $I[f,\varphi]$ can be minimized with respect to b_1 and b_2, while b_0 can be chosen so as to assure a perfect match between the approximated and true survival probabilities (i.e. $p(a) = \bar{p}(a)$), which corresponds to the third condition given in the text.

The pdf's in the formula of $I[f,\varphi]$ (equation (17)) are substituted by their corresponding equations to obtain, after cancellations:

$$\begin{aligned} I[f,\varphi] &= \int_{-\infty}^{\infty} [-F(S(x)-b_0-b_1x-b_2x^2) + \ln(\tilde{p}) - \ln(p)] \\ &\qquad \times f(x|\text{fish survives})dx \\ &= -F \int_{-\infty}^{\infty} [S(x)-b_1x-b_2x^2]\, f(x|\text{fish survives})dx \\ &\qquad + \ln \int_{-\infty}^{\infty} e^{-F(b_1x+b_2x^2)} \varphi(x|\text{a})dx - \ln(p). \end{aligned}$$

Necessary conditions for a minimum of this function are found by setting $\partial I[f,\varphi]/\partial b_1$ and $\partial I[f,\varphi]/\partial b_2$ equal to zero. These give, respectively,

$$0 = F \int_{-\infty}^{\infty} xf(x|\text{fish survives})dx - F\,\frac{\int_{-\infty}^{\infty} x \exp\{-F(b_1x+b_2x^2)\}\varphi(x|a)dx}{\int_{-\infty}^{\infty} \exp\{-F(b_1x+b_2x^2)\}\varphi(x|a)dx}$$

$$0 \doteq F \int_{-\infty}^{\infty} x^2 f(x|\text{fish survives})dx - F\,\frac{\int_{-\infty}^{\infty} x^2 \exp\{-F(b_1x+b_2x^2)\}\varphi(x|a)dx}{\int_{-\infty}^{\infty} \exp\{-F(b_1x+b_2x^2)\}\varphi(x|a)dx}.$$

These conditions are equivalent to the first two given in the text, which state that the first and second moments of the "true" and approximated pdf's should match. To verify that these are also sufficient conditions for a minimum, we see that

$$\frac{\partial^2 I[f,\varphi]}{\partial b_1{}^2} = F^2 [E[x^2] - E[x]^2] = F^2 E[(x-E[x])^2]$$

$$\frac{\partial^2 I[f,\varphi]}{\partial b_2{}^2} = F^2 [E[x^4] - E[x^2]^2] = F^2 E[(x^2-E[x^2])^2]$$

$$\begin{aligned} \frac{\partial^2 I[f,\varphi]}{\partial b_1 \partial b_2} &= F^2 [E[x^3] - E[x^2]E[x]] \\ &= F^2 E[(x-E[x])(x^2-E[x^2])] \end{aligned}$$

where $E[\cdot]$ denotes expected value of $[\cdot]$, computed with respect to the approximated posterior density. Clearly, $\partial^2 I[f,\varphi]/\partial b_1^2$ and $\partial^2 I[f,\varphi]/\partial b_2^2$ are both >0. Also, using the Cauchy–Schwarz inequality (Bickel and Doksum 1977), it can be shown that

$$\left[\frac{\partial^2 I[f,\varphi]}{\partial b_1 \partial b_2} \right]^2 - \frac{\partial^2 I[f,\varphi]}{\partial b_1^2} \frac{\partial^2 I[f,\varphi]}{\partial b_2^2} < 0,$$

which guarantees that the extreme is in fact a minimum.

Appendix IV. Derivation of Estimation Theory

Here we derive the likelihood function for all observations made of the catch in a given year. Observations consist of a random sample of individual lengths, a stratified random subsample of individual age-at-lengths, and the total in biomass.

Let N be the number of individuals in the random sample of individual lengths and let x_i be the log-length of the ith sampled fish. If the N observations are considered independent (i.e. neglecting the fact that the sample is taken without replacement), their joint density is

$$\text{(IV.1)} \quad f(x_1,\ldots,x_N|t) = \prod_{i=1}^{N} f^c(x_i|t)$$

where $f^c(x_i|t)$ is given by (16). Suppose that fish in the first sample are classified into S size categories and that a random subsample is taken from each stratum for ageing. Let N_s and NA_s denote, respectively, the number of individuals present and the number of individuals in the subsample in the sth category. Let a_k and x_k be the age and log-length of the kth individual sampled from the sth category. Outcomes within any given category are independent with joint probability

$$\text{pr}(x_1,a_1,\ldots,x_{NA_s},a_{NA_s}|t) = \prod_{k=1}^{NA_s} \text{pr}(a_k|x_k,t)\text{pr}(x_1,\ldots,x_{NA_s})$$

where $\text{pr}(a|x,t)$ denotes the conditional probability of a given x and $\text{pr}(x_1,\ldots,x_{NA_s})$ corresponds to the probability of choosing one particular combination of log-length values out of the $\binom{N_s}{NA_s}$ possible. Let a_j and x_j denote the age and log-length of the jth individual sampled for both age and length. By Bayes theorem:

$$\text{pr}(a_j|x_j,t) = \frac{f^c(x_j|a_j,t)P^c_{a_j,t}}{f^c(x_j|t)}\ .$$

The joint probability of all NA observations in this second sample is, then,

$$\text{(IV.2)} \quad \text{pr}(x_1,a_1,\ldots,x_{NA},a_{NA}|t) = \prod_{j=1}^{NA} \frac{f^c(x_j|a_j,t)P^c_{a_j,t}}{f^c(x_j|t)} \prod_{s=1}^{S} \frac{1}{\binom{N_s}{NA_s}}\ .$$

The log-likelihood associated with all sampling observations is the logarithm of the product of (IV.1) and (IV.2), which, up to additive constants, is the sum of two components:

$$\sum_{i=1}^{NS} \ln[f^c(x_i|t)]$$

where NS is the number of fish measured but not aged and

$$\sum_{j=1}^{NA} \ln[f^c(x_j|a_j,t)P^c_{a_j,t}].$$

The third component of the log-likelihood (19) is a normal density approximation of the pdf for the total catch in biomass Y_t. We need to derive the mean $E_Y(t)$ and variance $V_Y(t)$ of Y_t, given that we know the size of measured fish. First note that Y_t is the sum of the individual weights of all the $C(t)$ animals in the catch, which can be decomposed into sampled and not sampled animals. Accordingly,

$$\text{(IV.3)} \quad E[Y_t|C(t)] = E[\sum_{i=1}^{C(t)-N} W_i(t)|C(t)] + E[\sum_{j=1}^{N} W_j(t)|x_1,\ldots,x_N]$$

where $E[(\cdot)|(\cdot\cdot)]$ denotes the expected value of $(\cdot)$ conditional to $(\cdot\cdot)$ and $W_i(t)$ is the weight of the ith animal in the catch. The derivation of the unconditional mean and variance of Y_t is most easily accomplished by using the relationship between conditional and unconditional means and variances. Specifically, we use the theorem (Bickel and Doksum 1977) that for any two random variables u and v,

$$E[u] = E[E[u|v]]$$
$$V[u] = E[V[u|v]] + V[E[u|v]].$$

In our applications of this theorem below, $[C(t)-N]$ takes the role of v and $\Sigma_{i=1}^{C(t)-N}\ W_i(t)$ takes the role of u.

We assume a weight–length relationship of the form

$$W_j = mL_j^r e^v = me^{rx_j+v}$$

where $v \sim N(0,V_v)$ and r and m are parameters. The unconditional expectation of Y_t, derived from (IV.3), then becomes

$$E_Y(t) = (E[C(t)] - N)E[W(t)] + mE[e^v]\sum_{j=1}^{N} e^{rx_j}$$

and the variance of Y_t is given by

$$V_Y(t) = (E[C(t)] - N)V[W(t)] + E[W(t)]^2V[C(t)] + V[e^v]m^2\sum_{j=1}^{N} e^{2rx_j}$$

where

$$E[C(t)] = \sum_{a=0}^{A} E_N(a,t)[1-p(a,t)]$$
$$V[C(t)] = \sum_{a=0}^{A} (E_N(a,t)[1-p(a,t)]p(a,t) + [1-p(a,t)]^2V_N(a,t))$$

are, respectively, the expected value and variance of the catch in numbers, summed across the age-specific values, as derived from (11) and (14). The expected value of the weight of a fish chosen at random from the catch is

$$E[W(t)] = mE[e^v]\sum_{a=0}^{A} P^c_{a,t}\int_{-\infty}^{\infty} e^{rx} f^c\,(x|a,t)\,dx$$

where

$$\begin{aligned}\int_{-\infty}^{\infty} e^{rx}f^c(x|a,t)dx = \frac{1}{1-p(a,t)}\Bigg[&\exp\left\{rE_x(a,t) + \frac{r^2V_x(a,t)}{2}\right\}\\ \text{(IV.4)} \quad &-p(a,t)\exp\left\{rE_x(a+\tau,t+\tau) + \frac{r^2V_x(a+\tau,t+\tau)}{2}\right\}\Bigg]\Bigg]\end{aligned}$$

and its variance is

$$V[W(t)] = m^2E[e^{2v}]\sum_{a=0}^{A} P^c_{a,t}\int_{-\infty}^{\infty} e^{2rx}f^c(x|a,t)dx - E[W(t)]^2$$

where the integral on the right-hand side is as in (IV.4), with r replaced by $2r$. Expected values of e^v and e^{2v} and variance of e^v in the above equations are given by

$$E[e^v] = e^{V_v/2}$$
$$E[e^{2v}] = e^{2V_v}$$
$$V[e^v] = E[e^{2v}] - E[e^v]^2.$$

Appendix V. Glossary of Functions and Parameters

a = coded age where $a = 0$ corresponds to youngest age of exploitation

α = parameter of the stochastic growth model (1)

$\tilde{\alpha} = L_\infty\ (1-\rho)$

b_0,b_1,b_2 = coefficients of a polynomial approximation of $S(x)$

β = slope parameter of the stochastic growth model (1)

$C(a,t)$ = rv for number of individuals of age a in the catch in year t

$E_x(t)$ = mean log-length in the population of fish of ages $0 \leqslant a \leqslant A$ at the start of year t

$E_x(a,t)$ = mean log-length of a cohort of age a at the start of year t
$E_x^c(t)$ = mean log-length in the catch in year t
$E_x^c(a,t)$ = mean log-length in the catch of age a fish in year t
$E_N(a,t)$ = expected number of individuals in the population of age a at the start of year t
$E_N(t)$ = expected total number of individuals in the population of ages $0 \leqslant a \leqslant \mathrm{A}$ at the start of year t
$E_N^c(a,t)$ = expected number of individuals in the catch of age a in year t
$E_Y(t)$ = expected biomass of catch in year t
ϵ = normal growth rv with mean $E_\epsilon = 0$ and constant variance V_ϵ
$f(\cdot)$ = general notation for a pdf
$f^c(x|a,t)$ = pdf of log-length x in the catch in year t of given age a
$f^c(x|t)$ = pdf of log-length in the catch in year t
$F(t,x)$ = size-specific fishing mortality risk for year t
$F_{j,t}$ = full-recruitment fishing mortality risk for the jth gear type in year t
F_t = full-recruitment fishing mortality risk
K = Brody growth rate parameter
$l(a,t)$ = cumulative probability of survival from reference age 0 to age a
L_a = length of a given fish at age a
L_∞ = asymptotic length
λ = parameter used to define a family of growth models
Λ_t = logarithm of the likelihood function for all data in year t
Λ = joint log-likelihood of data collected for T years
m = parameter of the allometric weight–length function
m_2 = general notation for a second moment
$m_2^c(a,t)$ = second moment of (age a, year t) log-length in the catch in (13)
M = annual natural mortality risk
$N(a,t)$ = rv for number of individuals in a cohort who survive to age a in year t
$N(t)$ = rv for total number of individuals in the population of ages $0 \leqslant a \leqslant A$ at the start of year t
NA = number of fish measured and aged
NS = number of fish measured, but not aged
ν = normal weight rv with 0 mean and variance V_ν
$p(a,t)$ = probability a randomly selected individual avoids capture in year t
$P_{a,t}$ = probability a randomly selected fish in the population in year t is of age a
$P_{a,t}^c$ = probability that a randomly selected fish in the catch in year t is of age a
$\mathrm{pr}(\cdot)$ = denotes probability that event $(\cdot)$ occurs
$\varphi(x|a,t)$ = normal pdf with mean $E_x(a,t)$ and variance $V_x(a,t)$, evaluated at x
$\rho = e^{-K}$, discrete Brody growth coefficient
r = power coefficient of the allometric weight–length function
R_{t-a} = abundance of reference age 0 fish in year $t-a$
$S(x)$ = size x selectivity of fishing mortality
t = beginning of year t
$t + \tau$ = beginning of the second part of year t, after fishing
$\theta(i,a)$ = probability that a fish of true age i is said to be age a
$V_x(a,t)$ = variance of log-length of the cohort at age a at the start of year t
$V_x(t)$ = variance of log-length in the population at the beginning of year t
V_ϵ = variance of the normal growth random variable
$V_x^c(a,t)$ = variance of length in catch of age a fish in year t
$V_N(a,t)$ = variance of pdf for age-specific abundance in the population
$V_N^c(a,t)$ = variance of pdf for age-specific abundance in the catch
$V_Y(t)$ = variance of the pdf for Y_t
x_a = natural logarithm of length of an individual of age a
Y_t = biomass of total catch in year t

Carnivorous Suspension Feeding by the Subarctic Calanoid Copepod *Neocalanus cristatus*

Charles H. Greene[1]

Section of Ecology and Systematics, Corson Hall, Cornell University, Ithaca, NY 14853, USA and Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA

and Michael R. Landry[2]

School of Oceanography, University of Washington, Seattle, WA 98195, USA

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Carnivorous suspension feeding is described for the large subarctic calanoid copepod *Neocalanus cristatus*. This foraging mode relies on the use of a feeding current to entrain potential prey items and transport them into the copepod's capture area. The extensive use of a feeding current to entrain and transport prey into the capture area distinguishes carnivorous suspension feeding from the predatory modes typically described for other calanoid copepods. The consequences of carnivorous suspension feeding on *N. cristatus'* prey-selection patterns are significant. Feeding experiments reveal that the vulnerability of naupliar prey declines with increasing prey size, just the opposite result observed for other marine calanoids exhibiting more typical predatory feeding modes. The role of omnivorous feeding by *N. cristatus* within the pelagic ecosystem of the subarctic Pacific is also discussed. In contrast with earlier hypotheses, the results reported here are consistent with the emerging view that this large suspension-feeding copepod may be having at least as great an impact on the microzooplankton as on the phytoplankton of the region.

Le mode d'alimentation carnivore de type suspensivore du gros copépode calanoïde subarctique *Neocalanus cristatus* est décrit. Ce copépode crée un courant pour attirer les aliments dans son aire de capture. Le recours très fréquent à la création d'un courant pour le transport des proies permet de distinguer l'alimentation carnivore suspensivore des modes typiques de prédation observés chez les autres copépodes calanoïdes. Ce mode d'alimentation chez *N. cristatus* a d'importants effets sur la sélection des proies. Des tests d'alimentation ont révélé que la vulnérabilité des nauplius décroît à l'inverse de leur taille, ce qui est exactement le contraire de ce qui est observé chez les autres calanoïdes marins plus typiquement prédateurs. Il est également question de l'importance de l'alimentation omnivore de *N. cristatus* dans l'écosystème pélagique du Pacifique subarctique. Contrairement à d'autres hypothèses, les résultats dont il est fait état confirment le consensus naissant à l'effet que ce gros copépode suspensivore a peut-être autant d'effet sur le microzooplancton que sur le phytoplancton de la région.

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The feeding behavior of calanoid copepods has been the subject of intense research and considerable controversy (see reviews of Koehl 1984; Strickler 1984, 1985). Most of this attention has been focused on particle selection and the mechanisms of suspension feeding by which calanoids extract algae and other small particles from the water column. Far fewer studies have addressed prey selection and the mechanisms of carnivorous feeding by which calanoids capture active animal prey (but see Conover 1966; Gauld 1966; Lillelund and Lasker 1971; Ambler and Frost 1974; Kerfoot 1977, 1978; Lonsdale et al. 1979; Landry 1980, 1981; Paffenhofer and Knowles 1980; Wong 1981; Yen 1982, 1983, 1985; Greene and Landry 1985; Williamson and Butler 1986; Wong and Sprules 1986; Williamson 1987). Since the vast majority of marine calanoid copepods are omnivorous, both their herbivorous and carnivorous feeding tendencies deserve more equitable attention. Until recently, herbivorous grazing by calanoids typically has been equated with some type of suspension-feeding mode, while their carnivorous behavior typically has been equated with some type of predatory feeding mode. This simple dichotomy is no longer tenable (see Williamson and Butler 1986; Williamson 1987; this paper). Here, we describe a mode of carnivorous suspension feeding exhibited by the subarctic calanoid copepod *Neocalanus cristatus*. This feeding mode is distinctly different from

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[1] Author to whom correspondence should be sent (Cornell address).

[2] Present address: Department of Oceanography, University of Hawaii, Honolulu, HI 96822, USA.

TABLE 1. Feeding experiments conducted with *N. cristatus*.

A. Prey vulnerability experiments
Predator: *N. cristatus* (C5), $P = 2$ predators per jar (each preconditioned for 1 d without food)
Prey types: *C. pacificus* (eggs-C6)
Initial prey densities: $N_0 = 50$ prey per jar for nauplii
$N_0 = 25$ prey per jar for copepodites
Experimental replicates = 4, controls = 2
Experiment duration: $t = 1$ d (dark)
Jar volume: $V = 3.785$ L
Rotating wheel: 1 rpm
Temperature: 8°C

B. Functional response experiments
Predator: *N. cristatus* (C5), $P = 2$ predators per jar (each preconditioned for 1 d without food)
Prey types: *C. pacificus* (eggs-N6)
Initial prey densities: N_0 varied between 25 and 100 prey per jar
Experimental replicates = 10, controls = 2
Experiment duration: $t = 1$ d (dark)
Jar volume: $V = 3.785$ L
Rotating wheel: 1 rpm
Temperature: 8°C

the predatory modes described for other marine calanoid copepods and produces prey-selection patterns fundamentally different from those expected based on previous investigations of carnivorous feeding by marine calanoids.

Materials and Methods

Experimental Animals

Experimental animals were captured in vertical plankton tows from the deep waters adjacent to Friday Harbor Laboratories in the San Juan Archipelago region of Washington state. *Neocalanus cristatus* is endemic to the open ocean waters of the subarctic Pacific; however, expatriated populations are occasionally advected into the region through the Straits of Juan de Fuca. Although the species cannot complete its life cycle successfully in the region, expatriated individuals appear healthy after capture and feed readily in the laboratory.

Laboratory feeding studies were conducted with *N. cristatus* fifth copepodites (C5's), the final feeding stage in this species' life history (Heinrich 1962: Miller et al. 1984). In feeding experiments, *N. cristatus* C5's were offered the different developmental stages of *Calanus pacificus* as prey. Eggs, nauplii, and copepodid stages of *C. pacificus* were divided into 10 prey types: (1) eggs, (2) naupliar stages one and two (N1,2), (3) naupliar stages three and four (N3,4), (4) naupliar stages five and six (N5,6), (5) copepodite one (C1), (6) copepodite two (C2), (7) copepodite three (C3), (8) copepodite four (C4), (9) copepodite five (C5), and (10) copepodite 6 adult (C6). All naupliar and copepodid prey were raised from eggs at 12°C on a diet of *Thalassiosira weissflogii*. Although the different developmental stages of *C. pacificus* may be uncommon prey for *N. cristatus* in the subarctic Pacific, the results of this study do not bear directly on the energetics of *N. cristatus* in the field. We were interested only in examining the species' patterns and mechanisms of prey selection, and using a standard prey species like *C. pacificus* allows for easier comparisons with the results from other studies of carnivorous feeding by calanoid copepods.

Feeding Experiments

Two sets of feeding experiments were conducted to investigate the carnivorous behavior and prey selection exhibited by *N. cristatus*. In these experiments, *N. cristatus* C5's were offered fixed initial densities of each prey type. The procedures and conditions for these experiments are outlined in Table 1A. The second set of experiments was conducted to examine the functional response of *N. cristatus* to the range of prey densities commonly found in the oceanic waters of the subarctic Pacific (Dagg et al. 1984; Vidal and Smith 1986). In these experiments, *N. cristatus* C5's were offered varying initial densities of each prey type. Functional response experiments were conducted only with eggs and the naupliar prey types of *C. pacificus*; copepodid prey types were not included because feeding rates on these stages were low and not significantly different from zero. The procedures and conditions for these experiments are outlined in Table 1B.

The data from both sets of feeding experiments were used to calculate prey mortality rates and predator clearance rates according to the following equations:

$$(1) \quad N_F = N_0 e^{-mt}$$

$$(2) \quad F = \frac{V \cdot m}{P}$$

where F is the clearance rate (liters per predator per day), m is the instantaneous prey mortality rate (per day), N_0 is the initial number of prey per jar, N_F is the final number of prey per jar, P is the number of predators per jar, t is the experiment duration (days), and V is the volume of the experimental jar (liters). Use of the above equations assumes a constant clearance rate by the predator, an exponential decline in prey numbers throughout the experiment, and no accumulative loss in predator search time while handling prey. Although these assumptions may not be reasonable at higher prey densities, they were closely approximated at the densities in our experiments. This point is illustrated in Fig. 1 which shows that *N. cristatus*' clearance rates are essentially constant.

Behavioral Observations

The behaviors of *N. cristatus* and its prey were videotaped to provide insight into the mechanisms underlying the observed prey-selection patterns. Tethered individuals of *N. cristatus* were videotaped while feeding in a temperature-controlled (8°C) 0.075-L chamber. Untethered individuals of *N. cristatus* were videotaped while feeding in a 5.4-L chamber submerged in a temperature-controlled (8–10°C) 54-L aquarium. In the former case, a Panasonic videotape system (described by Greene and Landry 1985) was used with the camera mounted from above on a Wild dissecting microscope. In the latter case, the camera, equipped with a macrolens, was mounted on a tripod alongside the aquarium. In both cases, *N. cristatus* were observed when offered suspensions of the diatom *T. weissflogii*, the various naupliar prey types of *C. pacificus*, and combinations of both algal and animal food.

In a series of behavioral experiments, abilities of the different naupliar prey types to escape entrainment by a simulated feeding current were examined. The feeding current was simulated by drawing water through a pasteur pipette with the suction provided by a rheostat-controlled, single-piston vacuum pump. The flow conditions in the simulated current were adjusted to be of similar dimensions and velocities to those generated by tethered *N. cristatus* (Reynolds number range: 1.0–5.0). Capture efficiencies were calculated corresponding to the percentages of entrained prey that were captured by the

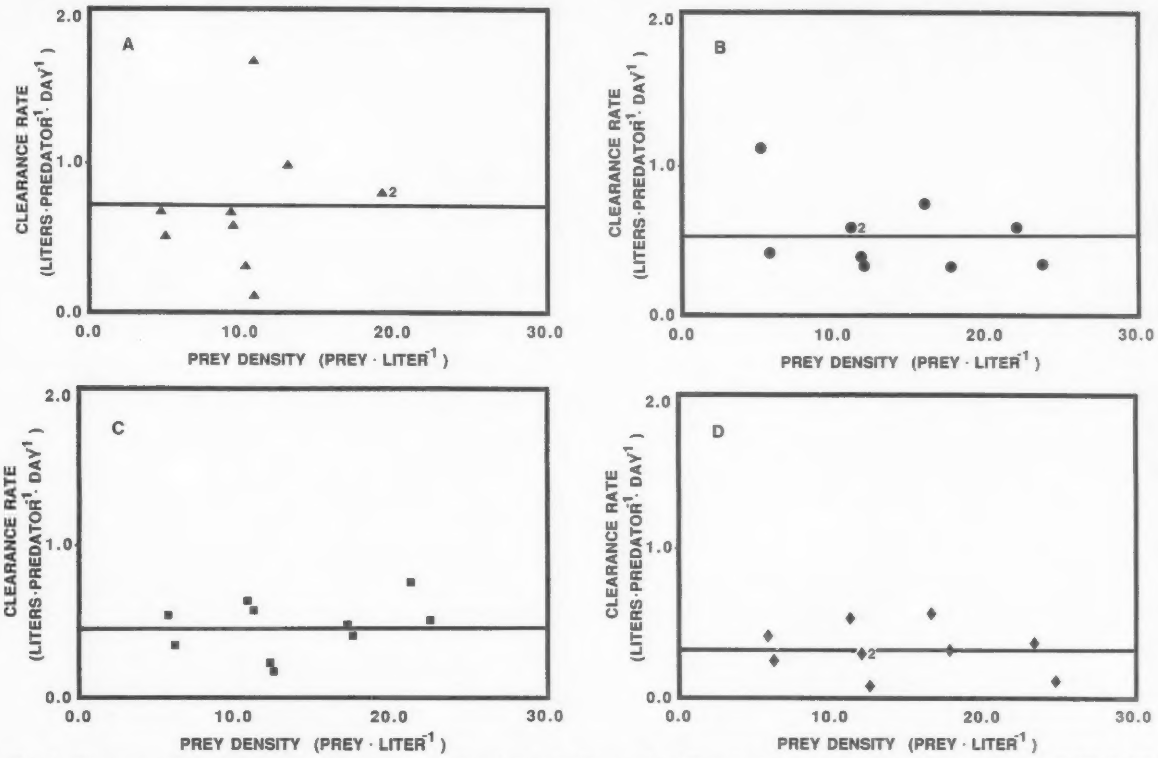

FIG. 1. Clearance rates as functions of prey density for *N. cristatus* feeding on the different prey types of *C. pacificus*. (A) Eggs; (B) N1,2; (C) N3,4; (D) N5,6. The correlations between clearance rate and prey density are not significant for all prey types examined ($P > 0.05$); therefore, the mean clearance rates are plotted as solid lines. The number 2 to the right of a symbol indicates two data points with identical values.

TABLE 2. Clearance rates of *N. cristatus* feeding on the different prey types of *C. pacificus*. Each clearance rate is the mean of four replicates. Mean clearance rates decline with increasing prey developmental stage (Spearman rank correlation coefficient, $r_s = -0.81$, $P < 0.01$).

Prey type	Clearance rate (standard deviation) (L·predator·d⁻¹)
Eggs	0.72 (0.44)
N1,2	0.46 (0.13)
N3,4	0.39 (0.24)
N5,6	0.30 (0.18)
C1	0.10 (0.15)
C2	0.02 (0.04)
C3	0 (0)
C4	0 (0)
C5	0 (0)
C6	0 (0)

simulated feeding current. All runs were videotaped under the microscope, and capture efficiencies were determined by playing back tapes one frame at a time (30 frames·s⁻¹). This procedure was necessary, since the human eye is incapable of keeping track of the rapid naupliar escape responses.

Results

Results from the feeding experiments reveal two key features of the carnivorous behavior exhibited by *N. cristatus*: (1) clearance rates decline on successively older developmental stages of *C. pacificus* ($P < 0.01$, Table 2) and (2) clearance rates remain constant on each of the prey types over the range of prey densities examined (i.e. the functional responses can be assumed linear) ($P > 0.05$ in each case, Fig. 1). Data from both sets of experiments were combined to determine values of the relative vulnerability index for each prey type (Greene and Landry 1985). This index is equivalent to the selectivity coefficient W' described by Vanderploeg and Scavia (1979) and is calculated by dividing the mean clearance rate for a given prey type by the mean clearance rate on the most vulnerable prey type ($\bar{F}_{\mathrm{eggs}} = 0.72$ L·predator⁻¹·d⁻¹). The trend in vulnerability as a function of prey developmental stage is illustrated in Fig. 2.

Videotaped observations reveal several qualitative features of *N. cristatus*' swimming and feeding behavior. This large copepod (total length: 7.1–8.9 mm, dry weight: 1.8 mg) is an infrequent swimmer, typically spending greater than 90% of its time hanging motionless in the water column. It is capable of producing a powerful feeding current with or without subsequent translational motion of the body. Food is entrained by this current and brought into the capture area (sensu Strickler 1982). No differences in the appendage movements associated with ingesting naupliar versus algal food could be distinguished; however, high-speed video or cinematography would be necessary to accurately record the detailed motions of these rapidly moving appendages (Strickler 1985).

The results from behavioral experiments examining the evasive abilities of different naupliar prey types are presented in

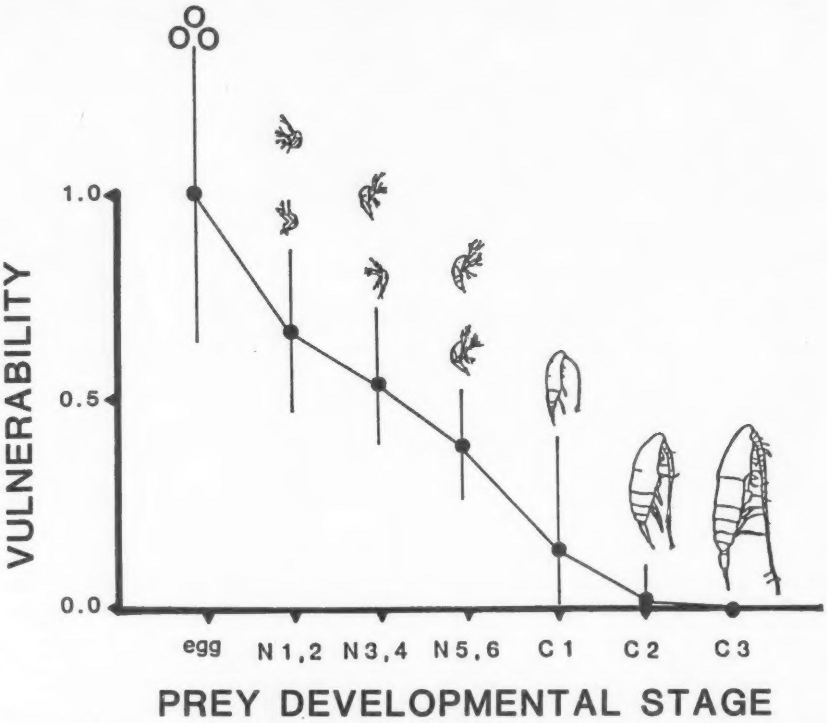

FIG. 2. Vulnerability of the different developmental stages of *C. pacificus* to carnivorous feeding by *N. cristatus*. Bars correspond to 95% confidence intervals.

TABLE 3. Comparison of the abilities of *C. pacificus* prey types to escape capture by a simulated feeding current versus their relative vulnerabilities to capture by *N. cristatus*. Capture efficiencies were determined from videotaped observations (*N* is the number of observations); 100% capture efficiency is assumed for the eggs.

Prey type	Capture efficiency (%)	Relative vulnerability
Eggs	100 (assumed)	1.00
N1,2	55 (N = 40)	0.64
N3,4	48 (N = 25)	0.54
N5,6	40 (N = 25)	0.41

Table 3. As might be expected, capture efficiency appears to decrease with increasing naupliar size.

Discussion

Neocalanus cristatus' Carnivorous Feeding Behavior

In previous descriptions of calanoid feeding behavior, the suspension-feeding modes used to extract small particles from the water column have been characterized as distinctly different from the predatory modes used to capture animal prey (see reviews by Gauld 1966; Strickler 1984; Greene 1988). While suspension feeding, many calanoids swim with a smooth, gliding motion that can often be punctuated with brief, intermittent pauses. This swimming behavior typically results from the high-frequency oscillations of three pairs of cephalic appendages: the second antennae, the mandibular palps, and the first maxillae, as well as a pair of thoracic maxillipeds. Feeding on small suspended particles is intimately associated with this swimming behavior, and the appendages used in locomotion are also involved with producing the "filtering" or "scanning" currents characteristic of most suspension-feeding calanoids (Cannon 1928; Lowndes 1935: Gauld 1966; Koehl and Strickler 1981; Paffenhofer et al. 1982; Cowles and Strickler 1983; Price et al. 1983; Strickler 1984, 1985). Although the mechanistic details of extracting particles from the "filtering" or "scanning" currents are controversial and vary among species, the production of a feeding current is a common feature that unites the behaviors of most suspension-feeding calanoids (see reviews by Koehl 1984; Strickler 1984, 1985; Price and Paffenhofer 1985).

In contrast with the suspension-feeding mode just described, many of these same calanoid species exhibit markedly different feeding behavior when taking animal prey. A successful predatory encounter typically commences when a prey item is perceived at a short distance away from the copepod, presumably sensed by mechanoreceptors on the copepod's first antennae (Landry 1980). When the copepod attacks, it reorients itself, seizes the prey with its second maxillae and maxillipeds, and then manipulates the prey into its mouth with the first maxillae (Gauld 1966; Williamson and Butler 1986; C. H. Greene and J. R. Strickler, pers. obs.). This predatory feeding behavior can be selective if (1) different prey types are encountered disproportionately, (2) different prey types are more susceptible to attack than others, and/or (3) the predator actively chooses and rejects certain types of prey (Greene 1983; Greene and Landry 1985).

Recent experimental studies with the calanoid copepod *C. pacificus* have revealed that the sensory stimuli and receptors used for the two modes of feeding are different (Landry 1980), that a switching response between the two modes can be elicited by altering the relative abundances of algal cells and copepod nauplii (Landry 1981), and that predation on copepod nauplii is selective, with prey vulnerability increasing with naupliar size (Landry 1980). These findings are consistent with the previous descriptions of calanoid feeding behavior, but provide several striking contrasts with the behavior exhibited by *N. cristatus*.

The most obvious behavioral contrast with previously studied calanoids is the infrequent swimming exhibited by *N. cristatus*. Typically, *N. cristatus* hangs nearly motionless in the water column, its sinking motion passively resisted by the drag of its greatly elongated first antennae. This energy-efficient means of maintaining its vertical position in the water column combined with occasional swimming bouts, perhaps in response to local food depletion and patchiness, may be adaptive features in the nutritionally dilute subarctic Pacific where *N. cristatus* is endemic.

Of greater significance from a trophic perspective, however, is the contrast between *N. cristatus*' feeding behavior and that previously described for other calanoid copepods. *Neocalanus cristatus* does not exhibit two distinct modes for bringing algal cells and nauplii into the working range of its mouthparts. Instead, videotaped behavioral observations reveal that the copepod uses a feeding current and hence a suspension-feeding mode when presented with algal cells only, nauplii only, or both. Thus, when nauplii are fed upon, they are entrained by the feeding current and brought into the capture area in the same manner as algal cells. At present, we are unable to determine whether nauplii in the capture area are collected raptorially or passively by *N. cristatus* (Price et al. 1983; Price and Paffenhofer 1984, 1985, 1986a, 1986b; Vanderploeg and Paffenhofer 1985). Price and Paffenhofer (1985) have reported that this species uses a "passive suspension-feeding mode" (note difference in their usage of this phrase from Jorgensen (1966)) when feeding on *T. weissflogii* (11–13 m). If *N. cristatus* detects and raptorially collects eggs and nauplii in the capture area, then this may help reconcile the higher clearance rates we observed with those reported by Frost et al. (1983) on natural particulates less than 30 μm.

In terms of *N. cristatus*' patterns of prey selection, the implications of carnivorous suspension feeding are great. Prey vulnerability declines with increasing naupliar size (Fig. 2), just the opposite result from that observed in *Calanus* and other calanoids exhibiting typical predatory feeding modes (Ambler and Frost 1974; Landry 1978, 1980; Greene and Landry 1985). In predatory interactions involving these other copepods, encounter rates with nauplii are the main determinants of prey selection. Hence, since larger nauplii are encountered more frequently, prey vulnerability increases with naupliar size (Landry 1980; Greene 1983; Greene and Landry 1985). In interactions with *N. cristatus*, the ability of nauplii to evade entrainment by the feeding current appears to be the main factor determining prey selection. Larger nauplii are more effective at escaping from a feeding current (Table 3), and thus, prey vulnerability declines with increasing naupliar size. These findings are analogous to the previously described differences in prey selection exhibited by particulate- and filter-feeding fishes (Drenner et al. 1982; Greene 1985). Prey selection in particulate-feeding fishes is shifted towards larger, more conspicuous prey due to biased perception by the predator during the encounter process. In contrast, prey selection in filter-feeding fishes is often shifted towards smaller prey that are less able to evade the gape of a filtering predator. Although unreported as yet, similar findings might be expected for other large omnivorous suspension-feeding crustaceans such as decapods, euphausiids, and mysids.

Despite the fact that we observed only carnivorous suspension feeding in *N. cristatus*, it should not be interpreted that this species never feeds in a predatory mode. Frost et al. (1983) have reported feeding rates for *N. cristatus* offered high densities (150 prey·L^{-1}) of *Oithona similis* copepodites that are difficult to reconcile with our observed rates. It may be hypothesized that *O. similis* elicits a predatory response in *N. cristatus* that we never observed. Alternatively, experimental artifacts associated with the unnaturally high prey densities they used may account for their results. Clearly, additional feeding studies with a wider variety of prey types and densities are necessary to test the above hypotheses.

Neocalanus cristatus' Trophic Role in the Subarctic Pacific

For some time, *N. cristatus* has been considered a potentially important suspension feeder on phytoplankton in the subarctic Pacific (McAllister et al. 1960; Heinrich 1962; Steele and Frost 1977; Fulton 1983). Only recently has its potential importance as a consumer of small zooplankton been recognized (Frost et al. 1983). The results from our study show that *N. cristatus* is very effective at suspension feeding on small, less evasive prey such as copepod eggs and nauplii. In this context, it is worth noting that many of the copepod species typically found to be abundant in the shelf and slope waters of the subarctic Pacific during spring and summer only become abundant in the open ocean waters after *N. cristatus* and its congener *N. plumchrus* have descended to diapause (Steele and Frost 1977; Batchelder 1985; Vidal and Smith 1986). The increase in abundance of these other species has been presumed to represent a release from competition with the *Neocalanus* species (Steele and Frost 1977). Alternatively, this increase may represent a release of these copepods' eggs and nauplii from predation by both *Neocalanus* species. At present, insufficient data are available to distinguish between these alternative possibilities, although it is recognized that both may contribute to the phenomenon. In either case, evidence is beginning to emerge that *N. cristatus* may be having at least as great an impact on the microzooplankton as on the phytoplankton of the subarctic Pacific (see Frost 1987).

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DNA-Level Polymorphism as a Tool in Fisheries Science[1]

Eric M. Hallerman[2]

Department of Genetics, The Hebrew University of Jerusalem, Jerusalem 91904, Israel

and Jacques S. Beckmann

Department of Plant Genetics and Breeding, Agricultural Research Organization, The Volcani Center, Bet Dagan 50250, Israel

Hallerman, E. M., and J. S. Beckmann. 1988. DNA-level polymorphism as a tool in fisheries science. Can. J. Fish. Aquat. Sci. 45: 1075–1087.

Several methods for the visualization of genetic polymorphisms at the nucleic acid level have been developed. Such polymorphisms promise to be exceedingly numerous, and may form the basis for a number of scientific and practical applications in fisheries science. An expanded number of genetic markers should increase the statistical power of marker-based studies in population genetics, for example, improving the sensitivity of biological stock assessments and of studies assessing the impact of stocking programs upon natural populations. Utilization of such genomic markers could contribute to the rapid elaboration of piscine genomic maps and to development of markers for health- and production-related traits in fishes.

Plusieurs méthodes ont été développées permettant la visualisation au niveau de l'ADN, de polymorphismes génétiques. De tels polymorphismes, qui promettent d'être extrêmement nombreux, serviront de base à de moultes applications, à la fois en recherches fondamentale et appliquée en ichthyologie. La nombre croissant de marqueurs génétiques devrait augmenter la puissance statistique d'études de génétiques de populations se basant sur ces marqueurs. Les moyens par lesquels l'utilisation de tels marqueurs génomiques devraient contribuer à une élaboration rapide de cartes génomiques des poissons et au développement de marqueurs associés à des propriétés de santé et de production se rapportant aux poissons, seront discutées.

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Fisheries scientists have utilized genetic markers as the basis for quantifying genetic relatedness among groups of fish in stock assessments among wild (Philip et al. 1983) and among cultured (Ryman and Ståhl 1980) populations and in studies of taxonomy (Buth 1984) and population genetics (Avise and Felley 1979). Although traditional blood group and allozyme markers served as the basis for many such studies, the limited numbers of polymorphic markers in the studied populations have frequently limited the power of such analyses.

The development of techniques for the manipulation of specific DNA fragments has provided the basis for uncovering a greatly expanded number of genetic markers based upon polymorphism of given DNA sequences. By offering virtually unlimited numbers of genetic markers, such techniques strengthen existing applications and make possible several scientific and practical applications not otherwise available. Although workers in fields such as medicine and agriculture have readily adopted DNA marker-based approaches, the fisheries community has not.

The objectives of this review are to describe the methodology and salient genetic qualities of the various classes of DNA-level markers, to outline means by which use of modern molecular genetics techniques might contribute to the achievement of certain broad objectives in fisheries science, and to identify some problems precluding rapid advancement toward attainment of these objectives.

DNA-Level Markers

Three general types of DNA-level markers may be distinguished, depending upon whether they are based on polymorphism of mitochondrial or nuclear DNA and on the means by which they are observed. Certain general qualities characterize all classes of DNA-level markers. Such polymorphisms are numerous and are well scattered about the genome. Mitochondrial DNA phenotypes are maternally inherited; polymorphisms of nuclear genomic DNA exhibit Mendelian inheritance, with codominant expression of alleles. DNA-level markers are largely unaffected by environmental or developmental factors. Marker phenotypes are sometimes informative as to the molecular basis of the observed variation (Fig. 1). Regarding methodological qualities, almost all tissues are suitable as a source of genetic material, and DNA samples may be stored for extended periods. The drawbacks of DNA-level

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[1] Contribution from the Agricultural Research Organization, The Volcani Center, Bet Dagan, Israel. No. 2171-E, 1987 series.

[2] Present address: Department of Animal Science, University of Minnesota, St. Paul, MN 55108, USA.

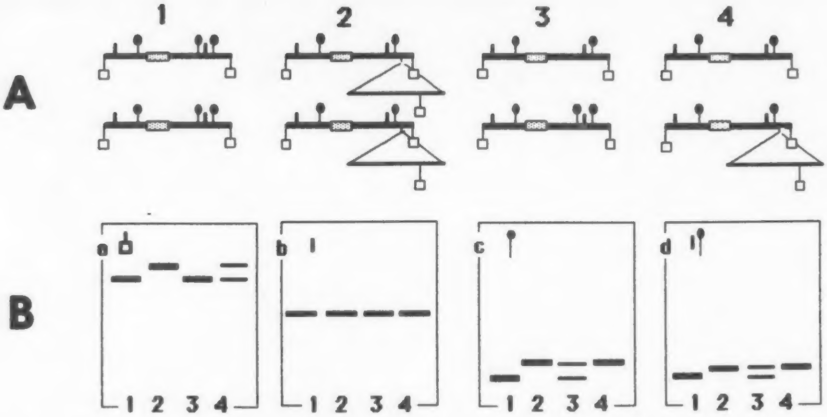

FIG. 1. Visualization of genomic restriction fragment length polymorphisms. (A) Representations of both complementary strands of a region of genomic DNA among four individuals, showing the distribution of restriction sites (open squares, vertical bars, and solid circles) in the vicinity of a particular probe DNA sequence (stippled box). The individuals differ with respect to presence or absence of a particular polymorphic restriction site (solid circle) or genomic insertion (horizontal bar joined to the DNA strands). Individuals 1 and 2 are homozygous for presence of the polymorphic restriction site and insertion, respectively. Individuals 3 and 4 are heterozygous for one of these variable characters. Following digestion of genomic DNA with restriction enzymes, electrophoresis in an agarose gel causes different-sized homologous fragments to lie at different distances from the migration origin. DNA is then transferred from the gel to a solid support, a membrane of nitrocellulose paper or treated nylon. (B) Visualization of polymorphism at or near a given probe sequence. A radiolabelled probe will hybridize (attach itself) to complementary DNA sequences bound upon the filter. Shown are the results obtained from autoradiography following hybridization of a probe for the sequence within the stippled box to the DNAs of these four individuals. (Adapted from Beckmann and Soller 1986b.)

TABLE 1. Generalized comparison of types of genetic markers.

Marker type	Scoring level	Extent of genome coverage	Sensitivity	Technical difficulty	Cost	Technical limitations
Morphology and meristics	Gross phenotype	Very limited	Low	Low	Low	Environmental influences
Isoenzymes	Expressed protein	Limited	Moderate	Moderate	Moderate	Small number of polymorphic loci
Mitochondrial RFLPs[a]	Mitochondrial genome	Extensive within mitochondrial genome	High	High	High	
Genomic RFLPs	Nuclear genome	Extensive	Unexplored in fish	High	High	Availability of suitable probes
Genomic OPs[b]	Nuclear genome	Quite extensive	Unexplored in fish	High	Moderate[c]	Knowledge of sequence polymorphisms

[a] Restriction fragment length polymorphisms.

[b] Oligonucleotide polymorphisms.

[c] Assuming knowledge of sequence polymorphisms.

markers as compared with protein-level markers are that they are relatively expensive in terms of materials and labor and that procedures for visualization of marker phenotypes are more demanding technically (Table 1).

Mitochondrial Polymorphisms

The methods utilized in visualizing restriction fragment length polymorphisms (RFLPs) of mitochondrial DNAs, aspects of sampling strategy, data analysis, and potential applications of such knowledge have been discussed previously (Lansman et al. 1981; Ferris and Berg 1987). These are briefly set out below for purposes of comparison vis-à-vis RFLPs of nuclear DNA.

Mitochondrial DNA (mtDNA) is isolated from total cellular DNA by purification of a satellite band following ultracentrifugation in a CsCl/ethidium bromide gradient. The mtDNA is then digested by restriction enzymes, which cut the DNA at specific recognition sequences, usually of four to six nucleotides. Depending upon the distribution of such restriction sites along the DNA molecule, this yields a mixture of restriction fragments of various sizes. Polymorphism in the mtDNA sequences among individuals leads to variability in the sizes of some of the restriction fragments so produced. Following enzymatic digestion, the fragments are separated electrophoretically in an agarose gel. The various restriction fragments in the gel may be visualized directly by staining the gel with ethidium bromide and viewing under UV light. Alternatively, fragments produced by restriction enzymes yielding staggered (i.e. uneven) ends may be end-labelled with ^{32}P (Brown 1980) and the gel incubated at −70°C with X-ray film, with polymorphism sought among the banding patterns so produced. A further technical alternative (Gonzalez-Villasenor et al. 1986) follows from the cloning of mitochondrial DNA of *Fundulus heteroclitus* and demonstration of its usefulness as a probe for Southern blot hybridization (see below) to total (i.e. genomic and mitochondrial) DNA from several other fish species. This procedure eliminates the expense and time of ultrapurification of mtDNA and allows the utilization of DNA prepared from frozen tissues.

The utility of RFLPs of mtDNA has been demonstrated in a range of applications in fisheries science. Minimal levels of mtDNA variability were taken to demonstrate the close relatedness of anadromous and nonanadromous forms of Atlantic salmon (Birt et al. 1986) and of Atlantic and Pacific skipjack tuna (Graves et al. 1984). Two highly distinctive morphs of mtDNA apparently related to recognized subspecies have been demonstrated in bluegill (Avise et al. 1984). MtDNA polymorphism has been used (Avise and Saunders 1984) to demonstrate interspecific hybridization and introgression in sunfishes of the genus *Lepomis*. MtDNA sequence divergence is greater between *Salmo gairdneri* and *S. clarki* than between the rainbow trout and steelhead trout forms of *S. gairdneri* (Wilson et al. 1985). MtDNA variability between *Anguilla rostrata* and *A. anguilla* showed that the two species were genetically distinct even though they spawned in close proximity (Avise et al. 1986). Large-scale size variation and heteroplasmy (variability within an individual) of mtDNA has been observed in bowfin (Bermingham et al. 1986). The extent of mtDNA variability in Great Lakes walleye seemed great enough to discriminate genetic stocks, and mtDNAs of closely related walleye and sauger were distinct enough to be used in studies of interspecific hybridization (Billington and Hebert 1986). MtDNA variability in broodstocks of lake trout could be used as markers for reproductive success of hatchery stocks planted in the Great Lakes (Grewe and Hebert 1986). Utilization of inter- and intraspecies variability in the mtNA of five salmonids for purposes of management and gene resource conservation has been reviewed by Gyllensten and Wilson (1987).

By virtue of the maternal mode of inheritance and rapid rate of evolution of mtDNA (Brown et al. 1979), screenings of widely distributed populations of given species might lead to insight into the origin and history of the species. Human mtDNA diversity studied in this manner (Cann et al. 1987) led to the inference that modern human populations can be traced back to a common female ancestor who lived in Africa some 150 000 – 300 000 yr ago. Although calibration of the rate of mtDNA evolution to an absolute time scale can be problematic (Stoneking et al. 1986), studies of piscine mtDNAs leading to inferences of the relative times and places where speciation events occurred might prove useful in confirming or refuting hypotheses in fish taxonomy and zoogeography.

Nuclear Genomic Polymorphisms

The methodology of visualizing RFLPs of nuclear genomic DNA (Fig. 1) reflects the complexity of the nuclear genome. In contrast with mtDNA, nuclear genomic DNA forms hundreds of thousands of different restriction fragments following digestion with a restriction enzyme. Upon electrophoresis, these produce a continuous smear in the gel. As a result, even if an RFLP were present, the resultant change in gel location of one or two restriction fragments could not be distinguished directly because many other fragments of approximately the same length will also be present at the same location in the gel.

Consequently, instead of looking at total DNA and attempting to detect RFLPs within the total mix of fragments, one looks for RFLPs by means of a specific cloned DNA sequence that can serve as a probe for restriction fragments bearing homologous genomic sequences. If a sequence polymorphism affects a restriction site within or adjacent to the genomic sequence hybridizing to the probe, the restriction fragment bearing the homologous sequence will differ in size among individuals, depending upon the presence or absence of the restriction site. These fragments will consequently migrate different distances through the gel upon electrophoresis. The DNA is then transferred (Southern 1975) to a nitrocellulose or nylon filter. Homologous DNA sequences bound upon the filter can then be detected by making use of their hybridization with a ^{32}P-radiolabelled (Rigby et al. 1977; Feinberg and Vogelstein 1983) or an enzyme-complexed (Renz and Kurz 1984) cloned DNA probe. An autoradiograph of the filter is then produced and inspected for the location of bands indicating the locations of the corresponding restriction fragments. Just as for mtDNA variation, RFLPs of nuclear genomic DNA are evident as bands lying at different locations from the migration origin in different individuals.

Genomic RFLPs have a number of genetic and methodological qualities rendering them particularly useful as genetic markers (Beckmann and Soller 1986a). Any unique or near-unique cloned DNA sequence can serve as a hybridization probe. The probe sequence does not have to be homologous to a known gene or to coding sequences. Furthermore, the restriction site polymorphism itself does not have to be within a coding sequence, but can be the result of sequence polymorphisms within exons (protein-encoding sequences), introns (noncoding sequences within given genes), spacers (noncoding sequences between genes), repetitive DNA, or regulatory sequences within or adjacent to the probe sequence. The restriction site polymorphisms may themselves be the result of point mutation, inversion, insertion, or deletion.

RFLPs are expected to be rather frequent in most populations. In studies of the human genome (Murray et al. 1984; Jeffreys 1979), it has been estimated that 1 in 100 base pairs is polymorphic and that about 1 in 100 of these is detectable using RFLP methodology. Assuming that a similar situation holds true among fish, tens of thousands of potentially detectable polymorphisms would be expected within a given species.

Although large numbers of RFLP markers have been demonstrated in well-studied species, the genome of fishes is virtually unexplored. Over 300 RFLPs have been detected in humans (Willard et al. 1985), and large numbers of RFLPs have been documented in laboratory species such as mouse (Bennett et al. 1982), *Xenopus laevis* (Martens and Herbert 1984), *Drosophila* sp. (Davis and Davidson 1984), and *Caenorabditis elegans* (Rose et al. 1982). Relatively few RFLPs have been found in other animals. To our knowledge, in only three studies have RFLPs of genomic DNA been reported in fish. A repeat-length polymorphism of ribosomal RNA genes has been reported (Popodi et al. 1985) in lake trout. RFLPs have been observed (Scott et al. 1985) among tandem repeats of antifreeze protein genes in winter flounder. Polymorphism of restriction sites within repetitive DNAs or in flanking sequences has been observed in three species of *Poecilia* (Monaco et al. 1985).

A systematic search through the literature revealed reports of about 50 cloned piscine genes. With no more than a handful of cloned genes for any particular species, the number of cloned homologous genes available for Southern blot hybridization and screening of populations of any particular species is limited. To some degree, heterologous sequences, that is, cloned DNAs from other species, may prove useful as hybridization probes in genomic screenings. Optimum conditions for hybridization and for washing of filters after hybridization would have to be developed separately for each probe. Heterologous probes have been routinely used in many applications in human (Chang et al. 1980), animal (Vaiman et al. 1986), and plant (Rom 1982) systems.

For purposes of developing numerous homologous probes, it is clear that in the near future at least, an alternative to cloned DNAs of known function will have to be utilized. Two technical alternatives are apparent. One would be to construct a library of cloned cDNAs (Maniatis et al. 1982) of unknown function from a tissue of interest. Such a library would contain clones devoid or largely devoid of repetitive DNA sequences which present a technical difficulty to informative Southern blot hybridizations. Screening of human DNAs with such random cDNA clones (Helentjaris and Gesteland 1983) identified a number of probes revealing RFLPs. Another approach would be to construct a library of random genomic restriction fragments (Maniatis et al. 1982) and to screen the library for fragments containing unique or near-unique DNA sequences (Wyman and White 1980). Methods have been developed (Litt and White 1985) for rapid screening of random genomic clones to identify those that are homologous to genomic regions that are especially rich in restriction fragment length polymorphisms.

Recent work in human genetics has documented the existence of ''hypervariable regions'' in genomic DNA. Potentially bearing any of a large number of alleles, a high level of heterozygosity is characteristically observed at such loci. Use of several human ''minisatellite'' (Jeffreys et al. 1985) probes revealed multiple loci of similar nature in mouse (Jeffreys et al. 1987), dog and cat (Jeffreys and Morton 1987), birds (Burke and Bruford 1987), and several agricultural species (J. Hillel, Hebrew University of Rehovot, Israel, unpubl. data). Use of these minisatellite probes allowed detection of multiple variable DNA fragments in fish (A. J. Jeffreys, J. Hillel, and D. B. Morton, unpubl. data, cited in Jeffreys and Morton 1987). Another group (Georges et al. 1988) has developed minisatellite probes revealing individual-specific banding patterns (''DNA fingerprints'') in barbel. It has been proposed (Chourrout 1986) to use DNA fingerprints to check for the absence of paternal genomic contribution in fish produced through gynogenesis (the production of fish through fertilization of the egg with deactivated sperm, retaining the second polar body to retain diploidity).

Hybridizations of Southern blots with a segment of wild-type phage M13 DNA (Vassart et al. 1987) revealed highly variable sequences in humans and in several animals. Although screening of piscine DNAs with M13 probes has not yet been attempted purposefully, it is noted that salmon sperm DNA had to be removed from hybridization solutions in order for the M13 probe to hybridize to DNAs from other species bound upon the filters, indicating that hybridization of this probe to fish DNAs had occurred.

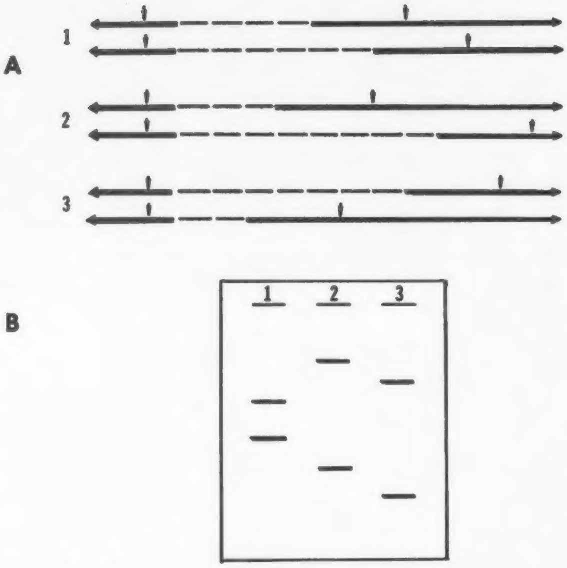

FIG. 2. Visualization of polymorphisms using a variable number of tandem repeats (VNTR) probe. (A) Representations of both chromosomal complements of homologous genomic regions of three individuals; each chromosome bears a different number of tandem repeats of a short DNA sequence. Restriction sites in flanking regions are indicated with arrows. DNAs from these individuals are restriction digested, electrophoresed in an agarose gel, and transferred to a filter. A DNA sequence from the repeating elements is radiolabelled and used as a hybridization probe. (B) Representation of the results of autoradiography of the hybridized filter. Many different allelic bands are revealed, reflecting different numbers of the tandem repeats among the various chromosome arms. Individuals are frequently heterozygous.

Methods (Fig. 2) developed for the detection of particular loci bearing variable numbers of tandem repeats (VNTR) of short sequences of human DNA (Nakamura et al. 1987) have not yet been attempted in other species. Hybridization of oligonucleotide probes (described below) specific for variations in the GA(T or C)A simple repeat family to human DNAs revealed numerous RFLPs (Ali et al. 1986). This family of repeated sequences is conserved through eukaryotes (Epplen and Ohno 1986), but screenings for polymorphisms of such sequences in fishes have not yet been attempted.

Oligonucleotide Polymorphisms

The visualization of DNA-level polymorphism by use of synthetic oligonucleotides (15–20 base-pair sequences of DNA) is a relatively new technique (Fig. 3) which has been utilized in research and diagnosis of human genetic diseases. Recent technological developments allow specified short DNA oligonucleotides to be obtained in large quantities and at moderate prices. The likelihood of a particular 18–20 base sequence occurring more than once in the genome by chance alone is near zero; under appropriate hybridization conditions, such oligonucleotide probes will anneal only onto a completely homologous sequence, while a mismatch of only one base pair will prevent hybridization. Thus, if DNA sequence information indicating specific allelic variants is available, allele-specific oligonucleotides (Erlich et al. 1986) can be produced and used to detect single-base modifications (Conner et al. 1983; Kaza-

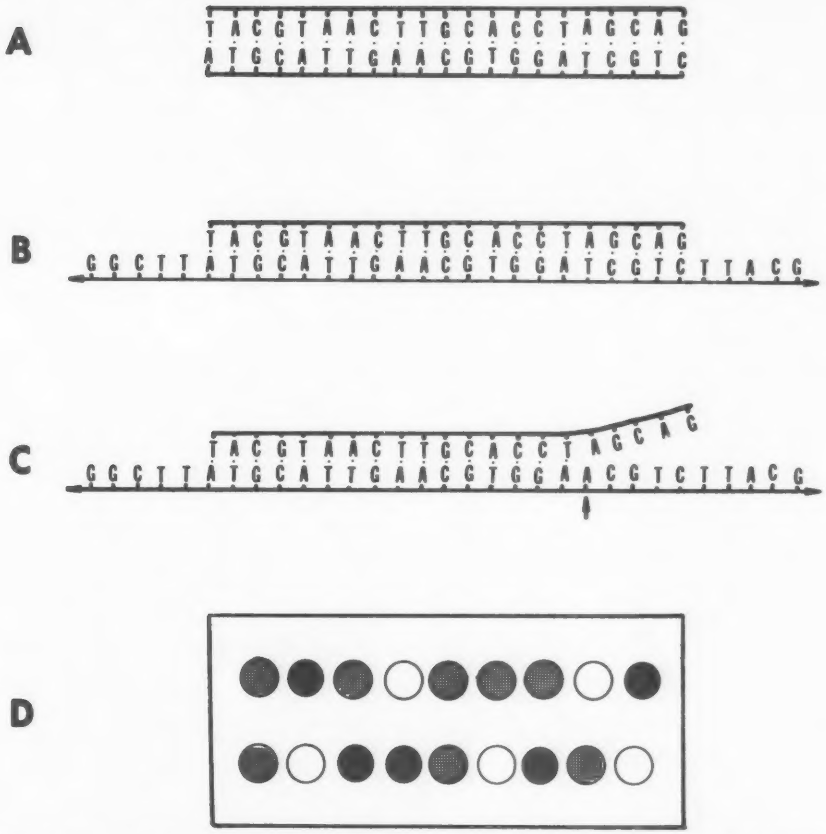

FIG. 3. Visualization of oligonucleotide polymorphisms. (A) A synthetic oligonucleotide is produced which corresponds to a short genomic sequence which is known or suspected to be polymorphic. The oligonucleotide is radiolabelled and denatured to single-stranded form. (B) The oligonucleotide will hybridize to a DNA bound upon a filter if there is perfect complementarity. (C) If a polymorphism exists which gives rise to a mismatch of even one base-pair (arrow), binding will not occur. (D) Such hybridizations may be carried out upon DNAs spotted onto a filter: a dot blot. Equal amounts of DNA are contained in each spot. Dark dots upon autoradiographs of the hybridized filter correspond to individuals homozygous for the DNA sequence shown in Fig. 3B. Dots with no bound radioactivity correspond to individuals homozygous for the sequence shown in Fig. 3C. Dots with intermediate levels of bound radioactivity correspond to heterozygotes.

zian 1985). By allowing virtually any point difference to be visualized, a limitation of RFLP methodology, i.e. that modifications must give rise to changes in the distribution of restriction sites, is overcome, greatly increasing the number of potential genetic markers.

Further, such oligonucleotide polymorphisms (OPs) can be visualized using dot blot procedures (Erlich et al. 1986). By eliminating the labor and expense of complete purification of DNA, enzymatic digestion of DNA, gel electrophoresis, and Southern transfer, the costs of marker screenings can be reduced dramatically. Additionally, several point differences within a particular genomic region might be visualized and considered together, the respective combinations being regarded as haplotypes which may be more informative than a single marker.

Utilization of DNA-Level Markers in Fisheries Science

DNA-Level Polymorphisms as Markers per se

The first and perhaps most important application of DNA-level polymorphisms would be simply as markers, to be added to the repertoire of morphological and meristic, blood group, and allozyme polymorphisms.

DNA-level polymorphisms might be found even in species where little or no protein-level variability has been observed (e.g. paddlefish; Carlson et al. 1982), opening up the possibility of marker-based studies where they were previously not possible. Moreover, increasing the number of markers screened will increase the power of statistical analyses of marker data.

Genetic variability within a population is usually considered in terms of average heterozygosity per locus (Nei and Roychoudhury 1974). Both theoretical (Nei and Roychoudhury 1974) and empirical (Gorman and Renzi 1979) studies showed that for estimating average heterozygosity per locus, $\hat{H}$, it was better to examine a large number of loci rather than a large number of individuals per locus. Nei and Roychoudhury (1974) demonstrated the trade-off between the number of loci screened (r) and the number of individuals screened per locus (n) by substituting published data into the expression for the sampling variance of $\hat{H}$, holding rn constant: the standard error of $\hat{H}$ decreased from 0.043 to 0.022 as r was increased from 17 to 67 and n was decreased from 79 to 20, while bias due to the lower n remained small. Using an empirical approach, Gorman and Renzi (1979) showed that a sample of 8–12 individuals yielded, on average, a heterozygosity estimate within 1% of the percent heterozygosity calculated for larger samples. In practice, on the order of 30 protein loci are screened in most surveys, while more than 50 (Nei 1978) should be screened to obtain a reliable estimate of average heterozygosity for the total genome. As such numbers of markers at the protein level are not generally scored, screenings for markers at the DNA level might be added to improve estimations of average heterozygosity.

Genetic relatedness of populations is measured (Buth 1984) by determining allele frequencies for a number of loci, converting such data into coefficients measuring genetic identity/distance (Nei 1972; Rogers 1972) among populations, and clustering such coefficients to visualize relationships among the populations studied. Genetic distance among populations (Nei 1972) is calculated as the arithmetic mean of all single locus genetic distances. Single locus genetic distances vary considerably between loci (Nei and Roychoudhury 1974). Loci that are either highly similar ($d < 0.01$) or highly different ($d > 0.9$) between pairs of populations tend to make most of the contribution to an estimate of genetic distance (Gorman and Renzi 1979); thus, a large number of loci should be screened to estimate the average genetic distance per locus. This has been demonstrated empirically by calculating genetic distance values upon data from given numbers of randomly drawn genetic loci within a larger data set (Gorman and Renzi 1979): large deviations from the distance values calculated upon the full data set were noted even when data from as many as 15 of the 22 loci were considered. The variance of single locus distance estimates over all loci, $V(d)$ (Nei 1978), includes both within-locus and between-loci components, and the variance of estimated genetic distance between populations is proportional to $V(d)/r$. The trade-off between the number of individuals to be examined and the number of loci screened is not simple to determine, as it is affected by the levels of heterozygosity within the populations at issue and upon the magnitude of the genetic distance itself (Nei 1978). However, unilaterally increasing the number of loci screened should reduce the standard error of the genetic distance estimate as a function of the square root of r.

Again, such numbers of loci are not available using blood or protein-level markers. Although the relatively high expense of screening for DNA-level markers precludes testing as many individuals as was customary for classical markers, this can be compensated for by increasing the number of loci tested.

The type of DNA-level marker used in studies of genetic distance (Cavalli-Sforza et al. 1986) is of great importance. Frequencies of polymorphisms visualized using clones of functional genes may be affected to an unknown degree by selection. Frequencies of polymorphisms visualized by use of random DNA clones should less frequently be affected by selection. Important clues regarding selection under, for instance, climatic or environmental conditions may be inferred by screening populations at functional gene loci. Selectively neutral markers, in contrast, are informative regarding the history of separation of populations because with such markers, genetic divergence will be a direct function of time.

Models distinguishing between selective and nonselective forces acting upon genetic variation among populations (Lewontin and Krakauer 1973; Robertson 1975; Schaeffer et al. 1977) are based upon the principle that natural selection will operate differentially upon each locus and upon each allele at a locus, while the effect of breeding structure (i.e. random drift) is uniform over all loci and alleles (Lewontin and Krakauer 1973). Utilization of such models entails statistical tests upon the collection of effective inbreeding coefficients, $\hat{F}_e$, calculated for each allele segregating in the studied populations. If all loci and alleles are selectively neutral, all such coefficients are estimates of the same underlying value, while if some or all of the loci or alleles are under selection, the various $\hat{F}_e$s will not be estimates of the same value, and the collection of effective inbreeding coefficients will be heterogeneous. In practical terms, the procedure involves deriving the distribution of $\hat{F}_e$ assuming that all values are indeed estimates of the same underlying value, and then testing for the significance of departures of the observed distribution of $\hat{F}_e$ values from that expected; for example, if the distribution of an allele's frequency is binomial or normal, tests are made of departures from the χ^2 distribution. Alternatively, the observed variance among $\hat{F}_e$ values may be compared with the theoretical variance (Lewontin and Krakauer 1973); selection is indicated if the observed variance is significantly greater than the expected. With typically no more than 20 blood group or isozyme alleles segregating within any given population, empirical determination of the underlying distributions of allele frequencies may be equivocal, decreasing confidence in results of tests of $\hat{F}_e$ distributions. Inasmuch as additional polymorphic loci would improve characterization of the underlying distributions of allele frequencies, the power of such tests would be improved. Also, heterogeneity can be more powerfully demonstrated within a larger collection of $\hat{F}_e$ values.

Marker-Based Screenings of Wild Fish Stocks

DNA-level markers have been utilized to establish relationships in recent studies of breeding structure in wild populations. By utilizing "DNA fingerprint" approaches developed in humans, it has been shown (Burke and Bruford 1987; Wetton et al. 1987) that particular house sparrows within the broods screened had not been fathered by the males guarding the nest. Using the markers previously available in the house sparrow, only about half of the cases of nonpaternity could be established. In a study of similar design, Quinn et al. (1987) constructed probes and screened for RFLPs in paternity/maternity analyses among lesser snow geese and found evidence of extra-pair mating and egg dumping. Studies of such design might prove useful in fisheries, for instance, in studying the reproductive success of "jack males," small, young male sunfish or salmon who sneak matings with females by entering the nests of larger, older males.

Marker-based methods have been utilized in assessing the relative contributions of component stocks in mixed-stock fisheries (e.g. Chilcote et al. 1980). General principles, applications, and data analysis for such studies have been reviewed by Pella and Milner (1987). The incorporation of DNA-level markers would provide additional observations of genetic variability in cases where isoenzyme studies have proven inadequate. In this regard, screening of mtDNAs might prove especially useful in uncovering alleles unique to or having widely differing frequencies among populations which have recently diverged (Ferris and Berg 1987).

Biochemical markers can be utilized in monitoring the effects of introductions of cultured fish into native populations (Moav et al. 1978; Chilcote et al. 1986). Suitable markers must be developed for given pairs of wild and domesticated stocks. Monitoring the effects of such introductions into the manipulated populations involves observing the segregation of marker haplotypes among individuals caught from the fishery and calculating the relative frequencies of the wild, domestic, and various hybrid and backcross components of the population.

DNA-level markers could be utilized to prove whether introduced males or females had spawned if strain-specific mitochondrial and genomic markers had been established and then monitored among young fish subsequently collected from the environment. Observation of young-of-the-year (YOY) fish bearing the genomic marker haplotypes characterizing the domestic stock but lacking the corresponding mtDNA markers would imply the spawning of the introduced males. Observation of YOY bearing both genomic and mtDNA markers from the domesticated stock in the absence of individuals bearing genomic markers only would imply the spawning of the females. Observation of both types would imply the spawning of both sexes.

Attributing a major portion of the reduction in average individual size in commercially exploited fisheries to selection for smaller, less catchable fish, Moav et al. (1978) suggested stocking of domesticated strains for the purpose of crossing with the wild stocks to produce heterotic F_1 hybrids, thereby upgrading the wild stock. Heterosis of the interstrain crossbreds between hatchery and wild stocks of salmonids for performance in natural waters has indeed been demonstrated (reviewed by Wohlfarth 1986). The effectiveness of such stocking programs could be monitored by observing marker haplotypes among individuals caught from the fishery. A particular marker would be especially useful if it had been linked as described below to an increasing quantitative allele in the domesticated stock, which was then introgressed into the wild population.

Beyond their usefulness as markers per se, nuclear genomic markers may form the basis for long-term projects approaching major objectives in fisheries science. Marker-based strategies for several such programs are described below.

Genetic Linkage, Genomic Mapping, and Genomic Evolution

Only three families of fishes, Salmonidae, Centrarchidae, and Poeciliidae, have been examined at all extensively in genetic linkage studies. Linkage data for pairs of isoenzyme loci have been collected for seven species of salmonids in the genera *Salmo*, *Salvelinus*, and *Oncorhynchus* (Johnson and Wright 1984). Eight enzyme loci have been examined for linkage in the centrarchid genus *Lepomis* (Morizot and Siciliano 1984). Among poeciliid genera, four enzyme loci have been assessed for linkage in *Poecilia*, 17 in *Poeciliopsis*, and 41 enzyme loci and two pigment pattern genes in *Xipophorus* (Morizot 1984). Such linkage relationships have been uncovered by utilizing genetic crosses within or between species to generate individuals heterozygous at two or more marker loci. In the classic design, linkage is assessed by crossing an individual heterozygous at two marker loci with an individual homozygous at both loci: a significant excess of parental-type individuals in the F_2 progeny constitutes evidence for linkage; the frequency of nonparental types provides an estimate of recombination between the loci, and hence an indication of their actual separation on the chromosome.

Three approaches to the expansion of existing piscine linkage maps have been suggested (Morizot and Siciliano 1984). Increasing the sample sizes of linkage comparisons already initiated or generating crosses to assess the possibility of linkages among previously untested pairs of enzyme loci each have the advantage of utilizing established strains of fish and well-characterized enzyme polymorphisms, but would seem unlikely to demonstrate many new linkage relationships. The third approach would be to introduce additional marker loci into assessments of linkage. In this connection, the development and utilization of DNA-level polymorphisms would add to the analysis of genetic linkage a number of markers far greater than that of available enzyme markers.

An efficient way to proceed may be to establish a standard cross between two strains or species to maximize the likelihood of polymorphism with any potential marker utilized. The DNA samples from several hundred F_2 individuals of the cross could be used as a standard collection for linkage mapping purposes. Once a polymorphism is detected with a given probe, the specific distribution pattern of allelomorphs among the F_2s would be used to locate the probe with respect to other sequences already mapped (Beckmann and Soller 1986a).

An alternative approach to expansion of piscine genomic linkage maps is to go beyond the classical test cross approach and to utilize modern techniques proven useful with other organisms. Screening of somatic hybrid cell lines has led to the construction of genomic maps in species where production of test crosses is impractical (Ruddle 1981). Somatic hybrid cell lines are produced when cultured cells of a species of interest are induced to fuse with those of another species. After a number of passages through the cell culture cycle, many of the chromosomes of the species of interest are lost from among those of the recipient species. Different subsets of chromosomes from the species of interest will remain in particular hybrid cell lines. The panel of hybrid cells is screened for the presence/absence either of gene products (e.g. isoenzymes) or of DNA sequences (by means of Southern blot hybridizations). High levels of concordance of the distribution of presence/absence of given markers among the panel of hybrid cell lines are taken as evidence of synteny, that is, occurrence upon the same chromosome.

A number of methods may be utilized for genomic mapping of cloned fragments of DNA which are not available for protein-level markers. Cloned genomic DNA fragments may be mapped onto particular chromosomes by in situ hybridization upon metaphase chromosome spreads (Evans and Atwood 1978; Harper and Saunders 1981). Techniques that facilitate the handling of chromosome-sized segments of DNA include chromosome sorting (Lebo et al. 1979; Griffith et al. 1984) and microdissection and microcloning of chromosomes (Fisher et al. 1985). Cloning of DNA fragments hundreds of kilobases in size can be carried out using yeast vectors (Burke et al. 1987), and pulsed field electrophoresis (Hardy et al. 1986; Lawrence et al. 1987) can be used to map the locations of genes within genomic sections of such size. Once a cloned gene has been mapped to a given chromosome, additional markers upon that chromosome can be developed by chromosome walking (Rohme et al. 1984) or chromosome hopping (Collins and Weismann 1984). Utilizing such techniques, the genomic map of a species of interest can in time be elaborated to any desired degree and the genome saturated with polymorphic markers. Development and characterization of the requisite hybrid cell lines and the technical difficulty of the various other methods currently limit use of these techniques.

The use of molecular genetics techniques could free the investigation of gene duplication (Ohno et al. 1968) from the technical constraints imposed by isozyme techniques, which are based upon visualization of functional gene products. Investigations are available wherever any member of a gene family has been cloned, greatly expanding the number of loci which can be studied. The nature of the duplication event, i.e. whether it occurred through tandem duplication or through polyploidization, can be determined utilizing any of the mapping techniques cited above. Further, the fates of all daughter copies of a particular gene, including nonfunctional pseudogenes, can be followed, so long as a moderate level of DNA sequence homology has been conserved. All such members of a gene family can be recovered from a genomic library, cloned, and characterized. This might clarify the mechanism of any gene silencing events (i.e. whether because regulatory sequences or portions of the structural gene were not duplicated, or whether the gene was expressed, but the gene product was nonfunctional) and lead to insight regarding the evolution of the gene family. Such studies of the human growth hormone (Moore et al. 1982), mouse alpha-globin (Leder et al. 1980, 1981), and human immunoglobulin IgC epsilon (Ueda et al. 1986) genes have suggested that tandem gene duplications and the occurrence of pseudogenes are not particularly uncommon in mammals. In fishes, where only isozyme-level work has been carried out, tandem duplication of isozyme loci has been considered a rare, or at least uncommon, event (Buth 1983). Whether tandem duplications of isozyme loci are indeed rare in fish or whether pseudogenes have been systematically overlooked by methods dependent upon expression of functional gene products is currently unclear. Varying levels of isozyme gene silencing have been observed in tetraploid fishes (Woods and Buth 1984), suggesting the possibility of contrasting mechanisms of gene silencing in different taxa. Such a hypothesis could be investigated by cloning and characterizing the key loci, overcoming the constraint of protein-based approaches to examine genetic loci through their functional products.

Analyses of nuclear DNA polymorphisms (Wainscoat et al. 1986), elaboration of linkage groups, evaluation of duplicated genes, and construction of detailed genomic maps for related fish species would allow insight into evolution within particular taxa. Issues of evolutionary interest include where, within given lineages, gene duplication and chromosomal rearrangement events had occurred. As genetic linkage and genomic mapping information becomes available for a broader range of species, a more detailed picture of the nature of piscine and vertebrate evolution would emerge. Among questions to be considered is whether linkage groups conserved among higher vertebrates (Womack and Moll 1986) are also observed among fishes. Should this prove to be the case, development of piscine genomic maps could proceed more rapidly.

Markers at Loci Mediating Immune Responsiveness, Disease Resistance, and Cell Growth

Marker-based approaches might be utilized in the investigation of health-related traits. Products of the major histocompatibility complex (MHC) genes are involved in immune response (Klein 1978). The MHC of mouse, and to a lesser degree of humans, have been characterized (Bell et al. 1986), and many of the component genes have been cloned. The genes of the HLA-D region (DP, DQ, and DR loci) code for class II antigens, transmembrane proteins involved in antigen recognition that are expressed on certain immunocompetent cells and that are highly polymorphic. Cloned HLA-D sequences have been used as heterologous probes to investigate the corresponding MHC loci in several domesticated animals (Vaiman et al. 1986), and recognition of RFLP haplotypes (Andersson et al. 1986; Lipkin 1987) has been achieved to varying degrees in some animals. Some avian and mammalian MHC sesquences have themselves been cloned and characterized.

To our knowledge, parallel work in fish has yet to be initiated. Indeed, it is an open question whether the piscine MHC is organized as in higher vertebrates. A first question would be whether heterologous MHC sequences bear sufficient homology to prove effective as hybridization probes for recognition of piscine MHC sequences. Should such heterologous probes not prove successful, a great deal of work would be needed to clone the relevant piscine genes to initiate this line of research.

Upon development of suitable MHC markers, individuals, families, and populations both resistant and susceptible to particular diseases could be screened for possession of given markers or marker haplotypes. Serological-level resistance/susceptibility markers in the MHC complex have been found in other animals, e.g. for bovine leukemia virus (Lewin and Bernoco 1986) and for Marek's disease of poultry (Hansen et al. 1967; Longenecker et al. 1976; Briles et al. 1977, 1983). DNA-level markers in the MHC complex have been found for a number of autoimmune diseases in humans (Cohen et al. 1984; Howell et al. 1986; Festenstein et al. 1986).

The MHC complex has also been linked to other biological processes (Edidin 1983), particularly to reproduction, in chicken (Simonsen et al. 1982), rat (Kunz et al. 1980), mouse (Goldbard et al. 1982), and pig (Rothschild et al. 1986). To our knowledge, the involvement of the MHC in reproduction of fish has not been investigated.

Other genetic loci play major roles in health, but have been characterized less thoroughly than the MHC complex. The immunoglobulin gene superfamily contains a variety of multigene families and single genes that include most of the receptors for the vertebrate immune response (Hood et al. 1985). Human T-cell receptors are heterodimeric integral membrane proteins composed of alpha- and beta-chains (Meuer et al. 1984). A high degree of polymorphism of human beta-chain (V_b) genes has been indicated (Concannon et al. 1986), and evidence of associations between certain V_b haplotypes and disease incidence has been presented (Hoover et al. 1986). Progress in characterization of immunoglobulin gene families and utilization of such knowledge in the human system should serve as a guide for parallel work in fishes.

Several families of oncogenes encode nuclear proteins essential in normal growth and division of cells. Xiphophorin fishes have been found to bear a high copy number of v-src and v-ras and a smaller number of c-myc oncogenes (Vielkind and Dippel 1984). Expression of such genes is normally repressed by population-specific and cell type-specific regulatory genes, but hybridization between populations or exposure to carcinogens leads to breakdown of gene regulation and development of neoplasia (Anders et al. 1984a, 1984b; Ozato and Wakamatsu 1983). Markers for population-specific regulatory regions could be developed and exploited to produce tumor-prone and tumor-free populations. Knowledge gained from study of xiphophorin fishes could contribute to the understanding of carcinogenesis in other taxa. The presence of the v-myc oncogene in rainbow trout has recently been confirmed through sequencing data (van Beneden et al. 1986).

Knowledge of susceptibility/resistance markers for a given disease in a cultured species could be applied in marker-assisted selection for immune responsiveness and disease resistance, as has been carried out for Marek's disease in chicken and for scours in pig (Gavora and Spencer 1983). Among the technical problems in linking markers to immune responsiveness and disease resistance is the difficulty in quantifying such traits. The applicability of marker-based schemes aimed at disease resistance is also limited by an insufficient understanding of resistance mechanisms; further, to assess the feasibility of marker-assisted selection for given species and diseases, we must first assess the heritability of such immune response and disease resistance (Gavora and Spencer 1983).

Identification of Loci Having Direct Effects or Linked to Loci Having Direct Effects Upon Quantitative Traits

Molecular variability at certain loci, for instance at genes coding for MHC complex glycoproteins or for protein hormones, might have direct physiological effects upon quantitative traits. Methods utilized for documenting the direct effect of a polymorphism in a cultured population have been discussed by Beckmann and Soller (1987). Cases where molecular variants have direct effects upon production are expected to be relatively uncommon. However, once a direct effect of a polymorphism upon a trait of economic importance has been determined, a few generations of selection will suffice to bring it to high frequencies. In addition, a direct effect-associated marker can readily be introgressed from one population to another through appropriate crosses. Although identification of direct effects would be difficult, the economic impact of such effects, once identified, might thus be great (Beckmann and Soller 1987).

Many studies in fisheries and in quantitative genetics generally have documented correlation of biochemical marker alleles to indices of productivity (Kirsipuu et al. 1972; Reinitz 1977; McIntyre and Johnson 1977). Such correlations are presumably due to the effect of a linkage disequilibrium between alleles at the respective marker and quantitative-trait encoding loci (QTL).

Experimental designs have been developed (Soller 1978; Soller and Genizi 1978; Soller and Beckmann 1982, 1983; Beckmann and Soller 1983) for screening one to several hundred prospective marker loci for linkages (i.e. indirect effects) to quantitative traits in cattle and utilizing such knowledge for purposes of marker-assisted selection (MAS). This entails statistical testing of the difference in the performance with respect to a given quantitative trait of two groups of half-sibs bearing the alternative marker alleles plainly inherited from their marker-heterozygous sire. A matrix of such paired comparisons is constructed for all possible marker × quantitative trait combinations. Significant differences in quantitative performance between the marker-defined groups are taken as indicative of linkage between marker alleles and segregating quantitative trait locus alleles. Practical elements of experimental design involve controlling for environmental, age, or other nongenetic components of performance and including enough observations to minimize sampling error. A field test of such design screening paternal half-sib progenies in dairy cattle (Geldermann et al. 1985) identified markers associated with milk yield and with milk fat content in two of three such progenies.

Quantitative performance of cultured fish is strongly affected by nongenetic determinants (Hulata et al. 1976), including significant maternal effects (Siraj et al. 1984). On a practical level, while the number of egg masses in an experimental hatchery is likely to be limiting, it presents no problem to maintain a number of reproductive ripe males. Experimental and practical considerations thus dictate that marker-QTL linkage assessments in fishes be carried out within maternal progenies.

The number of markers utilized in a screening is a primary determinant of the likelihood of detecting a given proportion of the QTL segregating within a given progeny. The number of randomly located markers needed to bring a given percentage of the genome to within 20 centiMorgans (cM) of a marker (Kashi et al. 1986) depends mostly upon the size of the genome in question and to a lesser degree upon the number and relative sizes of its component chromosomes. The sizes of particular piscine genomes in terms of recombination units are not known; however, noting the DNA content of typical piscine (1.5–3 pg) and mammalian (6 pg) cells (Sober 1970), we might expect that a typical piscine genome would include a corresponding proportion of the roughly 3000 cM in a typical mammalian genome. We might expect to require a similar proportion of the 120–150 (Kashi et al. 1986) randomly located markers needed to place 80% of a mammalian genome within mapping distance (20 cM) of a marker. Considered from another perspective, we would want at least one or two markers upon each chromosome arm, with on the order of 40 chromosomes in a typical piscine karyotype. The upshot of these considerations is that tens of markers would be needed to undertake a thorough marker-QTL linkage analysis. The demonstration of marker-QTL linkages in cattle using a smaller number of marker loci (Geldermann et al. 1985) indicates that screenings on a more limited scale can succeed in mapping a subset of the segregating QTL.

The power of the design depends also upon the number of individuals scored for markers whose records are included in the statistical analysis. The inclusion of more individuals decreases the standard error about the mean performance of a marker-defined group, and so increases the precision of the estimated difference in performance between the alternative marker groups. To include tens or hundreds of individuals in each marker group, screenings of hundreds to 1000 or 2000 individuals would be necessary, depending upon the nature of the marker loci screened (i.e. the degree of heterozygosity revealed) and the breeding design of the particular experiment. A quantitative assessment of the power of marker-based screenings for detection of quantitative trait loci (Hallerman et al., unpubl. data) showed that the number of QTL so identified was more responsive to the nature of marker loci than to the number of individuals screened. A large collection of highly polymorphic marker loci is thus a precondition for successful utilization of the linkage-based approach to detecting QTL.

The possibility of reproductive manipulations unavailable in mammals and the high fecundity of fishes gives rise to relatively powerful designs for detection of marker-QTL linkages in fishes. To varying degrees, these designs would be improvements over the dairy cattle paradigm because the effects of many different mates and of rearing the young in many different environments would not be at issue.

The possibility of gynogenesis (the parthenogenetic production of all-female progeny through manipulation of the fertilized eggs) offers a design in which the female's quantitative alleles are tested only against her own genetic background. In gynogenetic spawns, both chromosome complements in the offspring are maternally derived: each gynogenetic individual bears one chromosomal complement from the ovum and the other from the second polar body (Purdom 1969). At loci for which the mother was heterozygous, performance of all homogygous progeny screened may be utilized in statistical tests.

A related design is possible for species exhibiting protandry, that is, sequential hermaphroditism. In *Sparus aurata*, for example, cryopreserved sperm collected from a young male individual can be used to fertilize its own eggs after its metamorphosis into a female (H. Gordin, Mariculture Research Station, Eilat, Israel, pers. comm.). Tests of marker-QTL linkage are available at all loci where this individual was heterozygous.

In species where such reproductive manipulations are not a technical possibility, powerful experiments may be designed upon utilization of full-sib progenies. Tests of differences in marker-defined classes of progeny can be made for any marker at which at least one of the parents was heterozygous. This design would be more powerful than the dairy cattle experiment inasmuch as the effects of different mates and environments are not at issue. Further, marker-linked QTL alleles in either parent might be identified.

A final possibility is to produce maternal half-sib progenies by dividing a female's egg mass and fertilizing each sample with semen from a different male. This design is essentially no different from that of Geldermann et al. (1985), except that fewer mates would be utilized and all progeny could be reared in the same environment.

Once linkage phases of marker loci and QTL alleles are established within a given progeny, the selection of future spawners is made on the basis of choosing individuals bearing maximal numbers of increasing quantitative alleles. Screening of several progeny groups would allow detection of more QTL, might allow the elimination of some false effects, and would identify different increasing alleles which might hopefully be combined by crossing of the respective groups of fish. By screening and establishing markers for QTL in different strains or species, such markers might be utilized for purposeful introgression of marked genes from one strain or species into the other (Soller and Beckmann 1988). It is noted that even if the same marker loci are in linkage with the same QTL in different linkages, the phase of the linkage might be different. It is further noted that recombination between marker loci and QTL would decrease the power of the statistical tests and thus the accuracy with which spawners are selected (Smith and Simpson 1986). Such effects can be minimized by using marker brackets (Soller and Beckmann 1982) whenever possible.

The cost of carrying out screenings of hundreds or thousands of individuals at tens of marker loci underlines the importance of choosing the most powerful experimental design available for the species at issue and of screening highly variable marker loci. Technical advances in screening of Southern blots and advances in the use of oligonucleotide polymorphisms should improve the cost-efficiency of such experiments through reducing costs. However, the cost of even relatively modest designs restricts such screenings to species of commercial value.

Detection of Genomic Sites of Insertion of Introduced Genes

The dramatic growth of mice bearing introduced genes for growth hormone (Palmiter et al. 1982; Palmiter and Brinster 1985) or for growth hormone releasing factor (Hammer et al. 1985a) has suggested the utility of gene transfer techniques for genetic improvement of fish. A human growth hormone gene has been transferred into rainbow trout (Chourrout et al. 1986), and a number of other transfers into fish have also been attempted (Klausner 1985). Problems on a technical level (Hammer et al. 1985b) and difficulty in obtaining permission from regulatory authorities to test genetically engineered organisms in an open environment have impeded the development of transgenic animals. A very basic problem is that few genes giving rise to economic improvement have been identified as candidates for gene transfer.

Marker-based approaches could be developed as an adjunct to gene transfer to determine the genomic sites at which insertions took place. For example, the presence/absence of the introduced sequence within a panel of somatic hybrid cell lines (see above) could be compared with those with previously mapped markers. Such information would indicate whether such insertions had occurred randomly or nonrandomly within the genome. Marker-based approaches such as those described above might also contribute in identifying genes with desirable effects which might be candidates for gene transfer.

Perspective

Techniques for the visualization and utilization of DNA-level polymorphisms cited in this study have been developed largely in human and laboratory animal systems. Adoption of such methods by the animal breeding and population genetics communities is evident in the appearance in the literature of studies describing such polymorphisms and setting out means for utilization of such knowledge for the species at issue. The fisheries community has been relatively slow in adopting such methods, with the exception of screenings for mitochondrial DNA variability.

The fisheries community might benefit in several general ways from the extensive work carried out in other organisms and speed the advance of parallel knowledge in fishes. The first would be in making use of the techniques shown useful in other organisms, as in development of variable number of tandem repeat (VNTR) probes in fish using the technique developed in humans. The second would be in testing knowledge specific to other organisms for applicability in fishes, for instance, in determining whether gene linkage groups observed in mice and humans also exist in fish. The third would be in making use of the actual genetic material produced in studies of other organisms, for example, in using heterologous probes for recovery of piscine genes. The eventual product of the adoption and utilization of a range of nucleic acids level techniques might well be a revolution in our perception of fish genetics, such as that which occurred in the wake of adoption of isozyme techniques.

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NOTES

Effects of Climatic and Density-Dependent Factors on Year-Class Strength of *Coregonus lavaretus* in Lake Constance

Reiner Eckmann and Ursula Gaedke

Limnological Institute, University of Constance, P.O. Box 5560, D-7750 Konstanz

and Hans Johst Wetzlar

Regierungspräsidium Tübingen, Nauklerstr.47, D-7400 Tübingen, Federal Republic of Germany

Eckmann, R., U. Gaedke, and H. J. Wetzlar. 1988. Effects of climatic and density-dependent factors on year-class strength of *Coregonus lavaretus* in Lake Constance. Can. J. Fish. Aquat. Sci. 45: 1088–1093.

The influences of density-dependent and density-independent factors on year-class strength (YCS) of *Coregonus lavaretus* in Lake Constance were studied by multiple linear regression analyses for the period from 1962 to 1982. Meteorological conditions that lead to early thermal stratification of the lake in April are of prime importance for YCS and account for 41% of the total YCS variance. Zooplankton concentration during spring has no significant influence on YCS. The extensive stocking program on the lake (50–200 million larvae stocked per year) significantly supports YCS, but this relationship becomes apparent only after the influence of meteorological conditions are removed from the data. Conspecifics of age-classes 1 and 2 have a negative influence on the age 0 year-class, but the nature of this intraspecific competition remains unknown. No stock–recruitment relationship could be detected in this study. The final model includes five independent variables and accounts for 84% of the total YCS variance.

On a étudié les influences de facteurs dépendants et indépendants de la densité sur l'importance des classes annuelles (ICA) de *Coregonus lavaretus* dans le lac de Constance au moyen d'analyses de régression linéaire multiple pour la période allant de 1962 à 1982. Les conditions météorologiques qui mènent à une stratification thermique hâtive du lac en avril sont d'une importance primordiale pour l'ICA et expliquent 41 % de la variance totale de l'ICA. La concentration de zooplancton au printemps n'a pas d'influence significative sur l'ICA. Le vaste programme d'ensemencement du lac (de 50 à 200 millions de larves relâchées chaque année) contribue de façon significative à l'ICA, mais cette relation devient apparente seulement lorsque l'influence des conditions météorologiques a été enlevée des données. Les congénères des classes d'âge 1 et 2 ont une influence négative sur la classe d'âge 0, mais la nature de cette concurrence intraspécifique demeure inconnue. On n'a pu déceler dans cette étude aucune relation entre le recrutement et les stocks. Le modèle définitif comprend cinq variables indépendantes et explique 84 % de la variance totale de l'ICA.

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It is generally accepted that fish population size is influenced by both density-dependent and density-independent factors. The importance of density-independent, i.e. physical, factors on marine species has long been recognized because simple stock–recruitment models usually failed to explain the observed recruitment variability (Sissenwine 1984). In anadromous and freshwater species, however, the combined effects of physical and biological factors have been given proper attention only in recent years (Crecco and Savoy 1984; Crecco et al. 1986; Henderson and Brown 1985; MacLean et al. 1981). This approach has to our knowledge not yet been applied to any whitefish population.

The coregonids of Lake Constance offer an outstanding possibility to explore the effects of density-dependent and density-independent factors on year-class strength (YCS) because an extensive data base is available which results from numerous earlier studies and from a recent routine monitoring program. Several workers have attempted to explain YCS fluctuations of coregonids in this lake by simple one-factor analyses considering the following parameters: egg production as a function of parent stock size (Nümann 1973; Hartmann 1978), predation on larvae by perch (*Perca fluviatilis*) (Nümann 1967), cannibalism (Nümann 1973), food supply for first-feeding larvae (Einsele 1941; Elster 1944; Nümann 1967), and stocking of the lake with larvae after normal or delayed hatching (Nümann 1973; Todd 1986). No conclusive results were obtained, or hypothesized relationships have not been tested statistically for their significance. However, all authors coincide in one aspect: they regard the larval phase as the critical period for the establishment of a new year-class. Hartmann (1983a) was the first author who pointed out the importance of spring temperature and wind for YCS. He speculated that these physical factors influence the feeding success of larval whitefish.

The purpose of the present study was to use multiple linear regression models to describe the YCS of whitefish. Our approach was process-oriented and started from the hypothesis that absolute zooplankton concentration in early spring was a major variable responsible for the survival of coregonid larvae. The vertical distribution of zooplankton in the water column and hence prey availability was thought to depend on the thermal stratification of the lake. The latter is determined by meteorological conditions and therefore we included sunshine intensity and wind force as independent variables in the model. We further presumed that by considering these density-independent effects, a previously undetected stock–recruitment relationship might be unmasked and the effect of stocking might be revealed.

Materials and Methods

Fish yield data for the upper basin of Lake Constance are available since 1914. They are based on monthly catch reports of professional fishermen from all three countries which border the lake. Anglers' catches are not registered properly, but in the case of coregonids they are insignificant. YCS have been investigated by Elster (1944) for the years 1925–39. Since 1952 they have been routinely assessed by personnel of the Institute for Lake Research and Fisheries (ISF) at Langenargen. These estimates are based upon biweekly to monthly test catches using gill nets of legal mesh size (mesh bar 44 mm). Samples are analyzed with regard to age and body weight, which provides an estimate of catch composition by age-classes. Using the monthly fishermen's catch data, the number of individuals of a certain year-class which are harvested from the lake can then be calculated month by month. Thus, in the present study, YCS is used synonymously for virtual population. Despite this broad data base, the availability of meteorological data restricted the present study to only 21 recent years from 1962 to 1982.

Catch data refer to the pelagic spawning coregonid "Blaufelchen" (*Coregonus lavaretus*) alone, while the inshore spawning "Gangfisch" is not considered here. These coregonids are not now considered as species (Vuorinen et al. 1986) but are referred to as "forms." Moreover, effectively they are not managed separately; for example, the distinction made between the two forms in the hatcheries is unreliable. Therefore, the numbers of artificially hatched larvae of both forms are combined for the purpose of the present study. That part of the eggs that is incubated at low temperatures in order to postpone the time of stocking is not considered separately. This seems to be justified because there are not two distinct dates of stocking; stocking occurs more or less continuously throughout March and April. Hatched larvae are generally not fed in the hatcheries before introduction to the lake. The variable LARV thus comprises all hatchery-reared larvae stocked into the lake.

The routine assessment of YCS provides the data base for calculating the number of individuals per age group which are present in the lake at any given time (this approach does not account for natural mortality). The virtual number of fishes per age group which are present in the lake on January 1 was taken as a proximate estimate of the number of conspecifics that could influence the new year-class during spring. This estimate is not significantly biased by fishing because coregonid yields are generally low in spring.

Surface water temperatures are read daily at the mouth of Constance Harbour, located directly at the outlet of the lake. Meteorological data are from the German Meteorological Service, Constance weather station. Sunshine values are given as mean hours per day and month. Wind force was quantified by calculating the sum of the cumulative number of days per month with more than 6 Beaufort ($>10.8\ \mathrm{m \cdot s^{-1}}$) and the cumulative number of days per month with more than 8 Beaufort ($>17.2\ \mathrm{m \cdot s^{-1}}$). Data from Constance weather station, located on the western edge of the lake, might not reflect the small-scale climatic variability of the lake basin. Yet, these data can be taken as representative for the general climatic trends which influence the lake, and only these are thought to be of importance for the present study.

The concentration of soluble reactive phosphorous (SRP) (milligrams per cubic metre) at the time of spring turnover is taken as an index of eutrophication. Determinations have been performed by various authors, and the data were compiled by the ISF. Dissolved oxygen is measured once per month at the deepest part of the lake ($z_{\max} = 252$ m) about 1 m above the bottom. Although the oxygen supply for the coregonid eggs lying on the bottom might be lower, these are the best data available to characterize the incubation conditions in the lake. Zooplankton concentrations are assessed by ISF personnel two or three times per month on five transects with three stations each. All samples are enumerated for species and size-classes. For the present purpose, overall monthly means were calculated separately for all individuals >1 mm body length (without spine) and <1 mm. The latter size group is often claimed to be indispensable for first feeding coregonids (Hartmann 1983b). The complete data base for this study is given in Table 1.

All calculations were performed with the Statistical Analysis System (SAS). Assuming a multiplicative influence of the independent factors on YCS, multiple linear regression models were calculated with the natural logarithm of YCS as the dependent variable. The influences of single factors and their combinations on YCS were evaluated via the significance levels of the parameters for being nonzero and by comparing the percentages of total variance explained by the model (adjusted $R^2 \cdot 100$). As there were 21 yr with a complete set of observations for all important independent variables, models with at most six parameters were fitted to the data.

Results

Because we started from the idea that zooplankton availability is a key factor for larval survival, we first looked at the effects of temperature and wind on YCS. A stable thermal stratification and hence a zooplankton concentration in the upper water layers should be favoured by high temperature and low wind force. Mean surface water temperatures in April (WT4) accounted for about 27% of the ln(YCS) variance, while wind force in April (WIND4) accounted for nearly 25%. Both factors combined in one model explained about 40% of the total variance (Table 2). These two variables, however, are not independent from each other because the effect of strong winds, i.e. mixing of all or part of the water column, results in lower water temperatures. The variable WT4 thus represents the general

TABLE 1. Year-class strength (YCS) in thousands, mean hours of sunshine per day in March (SS3) and April (SS4) in h·d^{-1}, mean surface water temperature in April (WT4) in °C, wind force in April calculated as the sum of days with more than 6 Beaufort and days with more than 8 Beaufort (WIND4), soluble reactive phosphorous during spring turnover (SRP) in mg P·m^{-3}, average near-bottom concentration of dissolved oxygen for the months of December, January, and February (O_2) in mg·L^{-1}, number of zooplankton organisms smaller than 1 mm (SZ4) and larger than 1 mm (LZ4) body length in April in thousands·m^{-2}, virtual number of conspecifics of age-classes 1, 2, and 3 and more (C1Y, C2Y, C3Y) in thousands, and total number of larvae stocked into the lake (LARV) in millions.

Year	YCS	SS3	SS4	WT4	WIND4	SRP	O_2	SZ4	LZ4	C1Y	C2Y	C3Y	LARV
1962	251	4.6	7.0	6.4	15	17	7.8	388	74	1084	232	4	45
1963	1214	4.6	4.0	4.2	1	18	8.4	695	176	251	261	1	47
1964	94	1.8	5.4	5.7	7	35	6.5	398	100	1214	158	4	27
1965	94	3.4	3.9	3.3	12	36	6.4	388	77	94	1031	26	34
1966	391	4.7	4.6	6.7	7	39	7.4	402	149	94	94	132	81
1967	802	3.8	6.1	6.0	8	30	7.6	295	93	391	88	5	58
1968	1495	4.4	6.5	7.3	4	38	8.1	283	125	802	307	2	54
1969	265	2.6	5.2	5.8	12	39	6.6	313	102	1495	642	11	86
1970	113	3.3	3.7	4.5	11	46	7.2	192	70	265	1363	47	85
1971	1689	2.8	6.9	6.4	3	48	7.7	394	124	1133	256	379	117
1972	245	5.4	3.6	5.6	11	79	4.6	521	92	1689	102	4	66
1973	237	4.6	4.9	5.2	6	83	4.5	246	56	245	1534	21	72
1974	4460	3.6	7.3	9.3	3	84	6.5	991	130	237	230	281	139
1975	337	3.0	5.3	6.2	5	90	7.0	398	131	4460	220	21	75
1976	999	6.6	7.6	7.5	0	83	6.7	351	66	337	4295	33	149
1977	949	4.2	4.0	5.8	9	88	8.4	502	119	999	336	2405	197
1978	355	3.2	2.5	6.6	1	79	7.2	355	131	949	985	150	212
1979	767	2.9	4.7	6.1	9	98	8.2	152	50	355	932	157	208
1980	1321	3.2	4.5	5.8	5	88	7.9	249	113	767	352	137	166
1981	836	3.6	6.4	7.5	6	83	8.5	653	127	1321	682	43	145
1982	2940	4.7	6.7	5.9	9	83	9.0	293	103	836	1260	117	190
1983	—	4.0	4.8	5.6	15	76	7.4	246	103	2940	828	293	247
1984	—	5.3	6.5	6.1	4	70	8.0	186	51	350[a]	2918	187	279

[a] Predicted YCS for the year 1983.

TABLE 2. Percentages of total ln(YCS) variance (i.e. adjusted R^2 values·100) explained by linear regression models comprising one or more of the independent variables (for abbreviations, refer to Table 1).

WIND4					24.7
WT4					26.9
ln(SS4)					19.2
ln(SS3)					10.9
ln(LARV)					<0
COMPET					<0
WIND4	WT4				39.7
WIND4	ln(SS4)				41.2
WIND4	ln(SS4)	ln(LARV)			58.9
WIND4	ln(SS4)	ln(LARV)	COMPET		77.3
WIND4	ln(SS4)	ln(LARV)	COMPET	ln(SS3)	83.6

temperature increase of the upper water layers in spring plus the cooling effect of strong winds. To overcome this compliction and to use largely independent variables in the model, we substituted the natural logarithm of mean hours of sunshine per day in April (ln(SS4)) for WT4. Although ln(SS4) alone explained only 19% variance, ln(SS4) and WIND4 gave 41%. Contrary to our expectations, neither of the zooplankton fractions in March or April contributed significantly to the YCS variation. This was also true when these were combined with the physical variables WIND4 and ln(SS4).

The number of larvae stocked into the lake (LARV) had no significant effect on YCS when tested as the only predictor variable. But, when ln(LARV) was combined with the two physical parameters WIND4 and ln(SS4), the adjusted multiple R^2 value increased by about 19% (Table 2). It is in this step where the natural logarithm was found to be the appropriate form of the LARV variable indicating a linear dependence between YCS and stocking. The number of larvae stocked into the lake increased during the 1960's and 1970's from about 50 to nearly 200 million individuals per year. Therefore, the variable ln(LARV) could as well be nothing more than just a substitute for some general positive trend during the 21 yr under consideration. Such a trend might be the result of the eutrophication process which was most pronounced during these years. Eutrophication could have influenced YCS via an increase of plankton production in spring or a change in zooplankton community composition. We therefore tested the effect of SRP concentrations on YCS and found that the variable ln(LARV) cannot be substituted by SRP, nor was the three-parameter model (WIND4, ln(SS4), ln(LARV) improved by including the variable SRP.

Another argument that has often been raised refers to the negative influence of eutrophication on coregonid stocks via low oxygen concentrations (Braum and Quos 1981). Mean near-bottom oxygen concentrations for December, January, and February (O_2), i.e. the incubation period of the eggs in the lake, were tested for their influence on YCS. No significant correlation could be found, neither when the variable was tested alone nor as an addition to the three-parameter model.

Next, we examined the effect of older conspecifics on YCS. The virtual numbers of coregonids of age-classes 1 and 2 are summarized in the variable COMPET, where age-class 1 is weighted by a factor of 0.5 because its potential impact was regarded to be less severe. When this variable was added to the three-parameter model, 77% of the total variance was explained. The highly significant ($p < 0.01$) negative effect of this variable was responsible for the name COMPET(itors). The model was not further improved by incorporating the number of conspecifics of age-class 3 and older, either by including them into the competitor term or by treating them separately as an index for spawning stock size. This means that even after removing the influences of physical factors, stocking, and a presumed intraspecific competition, no stock–recruitment relationship was apparent.

After we had observed that the meteorological conditions during April were of prime importance, we detected that sunshine in March was of significant importance as well (Table 2). The reasoning was that a warming up of the lake in March surely would aid the build-up of a stable thermal stratification in April. Therefore, we finally included the variable ln(SS3) into the model:

$$\begin{aligned}\ln(\mathrm{YCS}) = &-0.104\ \mathrm{WIND4} + 1.910\ln(\mathrm{SS4})\\ &+ 0.986\ln(\mathrm{LARV}) - 0.0005\ \mathrm{COMPET}\\ &+ 0.962\ln(\mathrm{SS3}) - 1.147.\end{aligned}$$

All parameters were highly significant ($p < 0.01$), except for ln(SS3) ($p < 0.05$). The y-intercept of the regression line is not significantly different from zero. The residuals plotted versus predicted ln(YCS) did not deviate from normality.

The model was tested by using the generalized jackknife statistic (Gray and Schucany 1972). We omitted every third year from the 21-yr data set and used data from the remaining 14 yr to predict the YCS of the omitted years. This was done three times altogether, first omitting the years 1962, 1965, ..., then the years 1963, 1966, ..., and finally the years 1964, 1967.... In this way, every year was used twice as part of a data set for estimating the model parameters, and its YCS was predicted once from a model which was fitted independently from the data of that year. There were two main reasons for using this technique. One was the strong eutrophication of Lake Constance which took place during the period of investigation and which may have an impact on YCS even if there is no statistical evidence for it at the moment. Therefore, years from the whole time range were taken to fit the model. The other reason was that there should be an adequate number of observations to fit the model parameters. The predicted YCS from these three tests of the model are jointly compared with the observed YCS in Fig. 1. The small discrepancies between observed and predicted values all lie within the 95% confidence limits of the predictions. YCS for the years 1983 and 1984 are predicted from the general model. Accurate estimates of YCS for these years are not available at this time.

Discussion

The present study substantiates the concept that meteorological conditions which lead to thermal stratification of the lake during April favour the development of strong coregonid year-classes in Lake Constance. However, our starting idea that absolute zooplankton concentration was a relevant factor for YCS is not supported by the model. YCS is not significantly influenced by zooplankton abundance. Furthermore, YCS ($\times 10^3$) during the years 1962–82 (min. 94, max. 4460, mean 945) are not significantly different from those observed about 40 yr earlier (Elster 1944) (min. 151, max. 4066, mean 1144), although absolute numbers of zooplankton in April increased sevenfold to ninefold for the total and small fraction, respectively, during the last 25 yr. This may be regarded as additional evidence that zooplankton abundance at this time is not a decisive factor determining whitefish larval survival. However, on a lower overall level prior to eutrophication that took place from 1950 to 1975, zooplankton concentration could have influenced year-class success. The influence of the temperature regime on YCS of Lake Erie whitefish has been demonstrated by Lawler (1965). In this case, an early temperature decrease in fall down to the optimum incubation temperature of 0.5°C and a late temperature rise in spring are necessary conditions for the development of strong year-classes.

In the case of Lake Constance, we suggest that the influence of temperature per se is the key factor for larval survival and

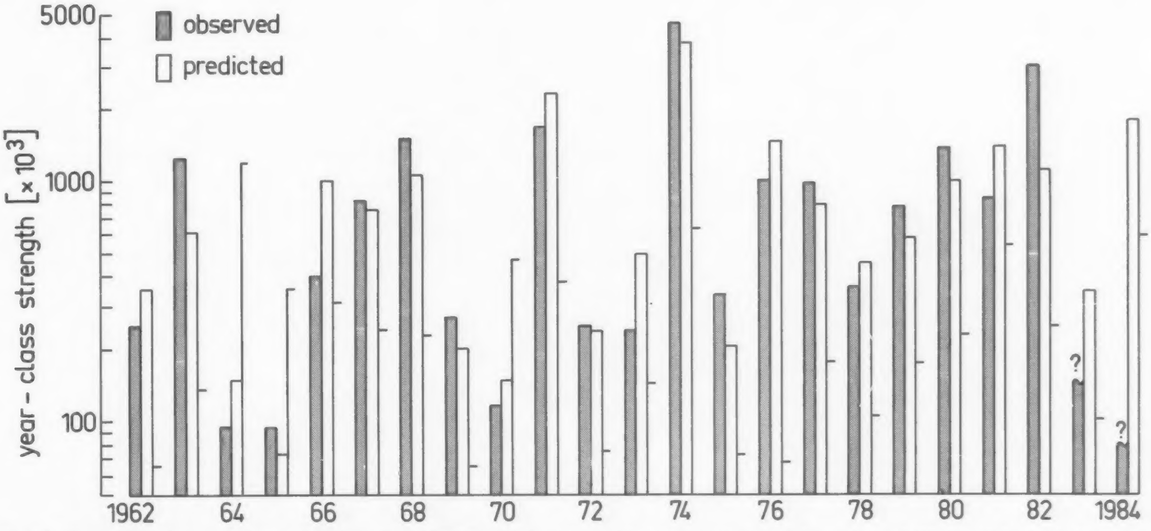

FIG. 1. Comparison between observed and predicted YCS for *C. lavaretus* of Lake Constance. The lower (upper) 95% confidence limits of the predictions are indicated by a horizontal tick on the right side of the open bars. The corresponding upper (lower) limit is symmetrical to this value. The predicted values were calculated from subsamples using the generalized jackknife statistic (see text for details).

hence YCS. This concept is supported by three factors based on early life history of coregonids in Lake Constance. Firstly, under calm weather conditions the coregonid larvae are not randomly distributed in the lake. They are found in the upper 1–3 m, and they are significantly concentrated near the lake shore (R. Eckmann, unpubl. data). Strong wind events may disperse the larvae considerably, but afterwards the typical near-surface, nearshore distribution is quickly reestablished. Thus, the larvae frequent a habitat where water temperatures can rise earliest in spring.

The second factor derives from feeding studies with coregonid larvae at 4, 8, and 12°C where freshly hatched *Artemia* nauplii were fed in excess to whitefish larvae (J. Ortlepp, University of Constance, unpubl. data). At 4°C, larvae recovered from an initial weight decline after 30 d, while at 8 and 12°C this lasted no more than 18 and 9 d, respectively. One hundred and fifty percent of the body weight at hatching was not yet reached after 40 d at 4°C, but was reached after 25 and 14 d at 8 and 12°C, respectively. Assimilation efficiency is obviously too low at 4°C, so that even a high-quality food such as *Artemia* nauplii does not lead to any significant increment in body weight during the first weeks of life.

The third factor is based upon a study of otolith ring patterns in wild larvae carried out in spring 1986 (P. Rey and R. Eckmann, unpubl. data). Almost all larvae that were caught before April 26 had otoliths that did not show any distinct daily increments or at most very narrow, low-contrast rings. These ring patterns suggest that all these larvae had either starved from the time of hatching or had ingested food but had not grown (Eckmann and Rey 1987). Most larvae sampled on May 7 or later showed broad, high-contrast daily increments. Back-calculating from these broad rings, larvae had started to grow around the May 1. From April 28 to May 6, total zooplankton concentration had not changed, but mean surface (0–3 m) temperature had increased from 5.9 to 9.8°C.

Our general conclusion about the influence of physical factors on YCS is, therefore, that high surface temperatures are mandatory for larval growth. Temperature influences growth directly via temperature dependence of metabolism. Other, indirect temperature effects seem to be of much less importance. The sooner the surface temperature rises in April, the sooner the larvae start to grow. Our model suggests that late onset of growth leads to low YCS. We suppose that the early onset of growth is advantageous for the larvae in two respects: firstly, they outgrow possible competitors, i.e. other larvae (mainly *P. fluviatilis*) which appear in the lake later in spring, and secondly, they are less vulnerable to predators if they grow faster.

Interestingly, the effect of stocking becomes apparent in the model only when it was included after the influence of density-independent factors was removed from the data. This means that all attempts to assess the influence of stocking on YCS without considering the key physical factors are bound to fail. Furthermore, the benefit of artificial incubation at low temperatures must be questioned. The theoretical advantage of this practice, that the larvae will find higher zooplankton concentrations at the time of stocking, is probably minimal. Firstly, because in recent years prey concentration is not a bottleneck for larval development, and secondly, because high concentrations of zooplankton are not apparently beneficial when water temperature is low. Consequently, delayed hatching by cold incubation will be most efficient when the larvae are stocked after the surface layers have already warmed. This implies that the larvae eventually have to be retained in the hatcheries and prefed with plankton or artificial feeds until mid-May.

The failure to detect any stock–recruitment relationship can in part be due to an inappropriate estimate of spawning stock size. Age-class 2 fish, which are included within the competitor term, are age 1+ during the spawning season in December of the previous year. Some whitefish in the eutrophied Lake Constance may spawn as early as age 1+, thus contributing to the total number of eggs spawned in the lake. According to a rough estimate of Hartmann (1978), the fraction of mature 1+ fishes may vary between 0 and 100% from year to year. However, because we have no reliable estimate of this figure, a stock–recruitment relationship cannot be further explored at the moment.

Similarly, the importance of conspecific competitors for YCS is not yet understood. Including age-class 3 into the competitor term does not improve the model significantly. The mode of interaction between the conspecific competitors and a new year-class could be via cannibalism, a behaviour which repeatedly has been claimed responsible for YCS fluctuations (Nümann 1973) but which has never been substantiated up to now. The only study where cannibalism in a whitefish population has been investigated (Skurdal et al. 1985) reports egg eating by adult whitefish in a river-spawning population. From echosurveys, we have information that most of the larger fishes of all pelagic dwelling species in Lake Constance stay in deep waters (30–60 m) during spring. They invade the upper water layers in late spring when the coregonid larvae have already started to grow. Cannibalism on first-feeding larvae is thus unlikely to occur, yet it might happen to older larvae and juveniles. As long as we have no convincing evidence for this, we would rather suggest an intraspecific competition to be more likely to occur, similar to the recent findings of Persson (1986) and Hanson and Leggett (1985). At any rate, some kind of feedback control of population size must exist, and the negative relationship between successive year-classes of whitefish in Lake Constance could reflect this regulation mechanism.

Finally it should be stressed that our model is of considerable analytical value because it permitted us to identify relevant factors whose combined effects on YCS would not have been unraveled otherwise. However, its predictive value is rather poor. The predicted mean YCS very closely follow the observed values, but the confidence limits of the predictions are rather broad (Fig. 1). Thus, the model should not be mistaken as a tool for fisheries management, but simply as an aid in understanding population dynamics.

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Contrasting Diel Patterns of Vertical Migration in the Dinoflagellate *Ceratium hirundinella* in Relation to Phosphorus Supply in a North Temperate Reservoir

W. D. Taylor, J. W. Barko, and W. F. James

Environmental Laboratory, Waterways Experiment Station, Vicksburg, MS 39180-0631, USA

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Very different diel patterns of vertical migration in *Ceratium hirundinella* were observed during two midsummer periods of study in a north temperate reservoir. During the first study (29–30 July), *Ceratium* migrated within a 2-m-deep oxygenated zone, moving upward near to the surface during the day and downward to the oxic–anoxic interface at night. During the second study (7–8 August), *Ceratium* did not migrate towards the surface during the day. High photosynthetic oxygen production and mixing processes increased oxygen distribution from 2 to 3 m providing *Ceratium* with access to a significantly greater water volume, with a greater nutrient content. Riverine phosphorus loading during the week prior to the first study was about 10 times greater than during the week prior to the second study. Limiting cell phosphorus concentrations and no measurable soluble reactive phosphorus in the upper (0–3 m) water column suggested a relationship between phosphorus limitation and the cessation of positive phototaxis. Diel patterns of vertical migration in this species may be influenced by episodic variations in phosphorus and/or other nutrient loadings via riverine inputs as interflows to this reservoir.

On a observé chez *Ceratium hirundinella* des régimes nycthéméraux très différents de migration verticale au cours de deux périodes d'étude au milieu de l'été dans un réservoir de la zone tempérée nord. Au cours de la première étude (29 et 30 juillet), *Ceratium* a migré à l'intérieur d'une zone oxygénée à 2 m de profondeur, montant près de la surface pendant le jour et descendant jusqu'à l'interface entre les zones oxique et anoxique la nuit. Au cours de la deuxième étude (7 et 8 août) *Ceratium* n'a pas migré vers la surface pendant le jour. Une production élevée d'oxygène par photosynthèse et les processus de mélange ont accru la distribution de l'oxygène de 2 à 3 m donnant à *Ceratium* l'accès à un volume d'eau beaucoup plus grand, ayant une teneur plus élevée en substances nutritives. L'apport de phosphore fluvial au cours de la semaine précédant la première étude a été environ 10 fois plus élevé que pendant la semaine précédant la deuxième étude. La limitation des concentrations de phosphore dans les cellules et l'absence de phosphore réactif soluble mesurable dans la partie supérieure (0 à 3 m) de la colonne d'eau portent à croire qu'il y a une relation entre la limitation du phosphore et l'arrêt de la phototaxie positive. Les régimes nycthéméraux de migration verticale chez cette espèce peuvent dépendre des variations épisodiques de phosphore et/ou d'autres charges de substances nutritives provenant d'apports fluviaux comme les écoulements divergents jusqu'à ce réservoir.

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As part of a continuing limnological study of Eau Galle Reservoir, Wisconsin, we have since 1981 investigated seasonal phytoplankton dynamics. The reservoir is dominated typically by just a few phytoplankton species during the year (Barko et al. 1984, and in progress). The diatom *Stephanodiscus hanzschii* Grun. forms large spring blooms, followed during the summer primarily by *Aphanizomenon flos-aquae* (L.) Ralfs and *Ceratium hirundinella* (O.F.M.) Schrank. Following a midwinter reduction in reservoir pool elevation, *Ceratium* during the summer of 1985 attained an exceptionally high population density (~90 $g \cdot m^{-3}$, maximum fresh weight) and for the first time in 5 yr of study totally dominated the system. In an attempt to reduce phytoplankton population density by controlling internal loadings of phosphorus, bottom sediments (the major phosphorus source during periods of hypolimnetic anoxia) were treated in late May 1986 by application of aluminum sulfate (Kennedy et al. 1987). This treatment provided a unique opportunity to investigate effects of phosphorus reduction on patterns of vertical migration in a near monotypic (*Ceratium*) phytoplankton community in a reservoir.

Patterns of vertical migration in this species have generally been related to nutrient and light availability, but are reported to be unaffected by thermal gradients (Frempong 1984). Motility provides the mechanism for traversing depth gradients to deeper water at night and then returning to an optimal light regime during the day (Talling 1971; Heaney 1976; George and Heaney 1978; Heaney and Talling 1980). *Ceratium* avoids anoxic water at depth and high irradiance conditions at the surface (Harris et al. 1979; Heaney and Talling 1980; Frempong 1984). Motility provides *Ceratium* access to a much larger portion of the water column and potentially greater nutrient supply than most other phytoplankton during periods of thermal stratification. Here, based on studies conducted in a stratified north temperate reservoir, we examine the association between phosphorus supply and diel migrational behavior in this species.

Methods

Studies were conducted during the summer of 1986 in Eau Galle Reservoir, a small, eutrophic, dimictic hardwater system located in west central Wisconsin. Eau Galle has a surface area of 0.6 km², a maximum depth of 9.5 m, and a mean depth of 3.6 m. This system receives runoff via riverine inflow from an agricultural drainage area of 166 km², about 280 times its surface area (Kennedy 1985). The Eau Galle River contributes 80–90% of the hydraullic load, while three lesser tributaries account for the remainder.

An open tube, 1 m in diameter and 4 m long, was constructed to isolate a water column, thereby providing a relatively quiescent environment compared with the open water. Heavy wire fencing (15 × 15 cm mesh) was used to form a rigid frame within which 6-mil polyethylene tubing was attached. The upper end of the tube was attached to an anchored float in the central basin of the reservoir. The tube was installed the day before diel studies were to begin, thus minimizing "enclosure effects" on phytoplankton community composition. The tube was long enough to extend well into the anoxic zone, effectively trapping the phytoplankton community.

A 3-m-long water sampler, used within the tube as well as in the open water, was constructed by running 6.5-mm inside diameter flexible plastic tubing through the center of a 10.3-cm-diameter plastic pipe. Separate lengths of tubing were connected to individual sampling ports, spaced at 25-cm intervals along the length of the pipe. Water samples (250 mL) were withdrawn with a peristaltic tubing pump from each port.

During the course of two diel studies, water samples were collected and a Hydrolab Surveyor II was used to characterize in situ profiles of oxygen and temperature. Five samplings were included during a 26-h period between 12:00, 29 July, and 15:00, 30 July, in the first study. Similarly, five samplings were included during a 31-h period between 17:00, 7 August, and 24:00, 8 August, in the second study. Samples were transported to a nearby field laboratory, and within 1 h, chlorophyll fluorescence was determined on unfiltered water using a Turner fluorometer, model 111. A strong linear relationship between chlorophyll *a* (determined according to procedures of Strickland and Parsons (1968)) and fluorescence ($r = 0.84$, $p < 0.001$, $n = 46$) supports fluorescence as a good estimator of chlorophyll concentration.

During the second study, soluble reactive phosphorus (SRP) was determined using the ascorbic acid method (American Public Health Association 1980). In addition, surplus cell phosphorus and phytoplankton dry weight were determined on samples from depths of maximum fluorescence. Surplus cell phosphorus was estimated as hot water extractable phosphorus (HEP) by modification of the method of Fitzgerald and Nelson (1966). Modifications included filtration using glass fiber filters (Gelman A–E) and then boiling of filters in distilled water for 1 h prior to analysis for phosphorus as above.

Results and Discussion

Phosphorus dynamics — Hypolimnetic (7–9 m) SRP concentrations during the summer of 1986 following aluminum sulfate treatment were greatly reduced 50–75% in comparison with earlier years (James et al. 1987; Kennedy et al. 1987). Thus, the watershed as opposed to sediment increased in importance as a source of phosphorus to the open water of Eau Galle during the summer. Moreover, the region experienced an unusually wet summer in 1986 (Fig. 1), contributing to a much greater than usual hydraulic load. Based on daily measurements of inflow from the Eau Galle River (U.S. Geological Survey, unpubl. data) and periodic determinations of SRP concentration in river water, phosphorus loading from the watershed during the week prior to the first study was about 10 times greater than during the week prior to the second study (7.6 and 0.7 mg $SRP \cdot m^{-2} \cdot d^{-1}$, respectively). SRP concentrations in the Eau Galle River ranged from 10 to 80 $\mu g \cdot L^{-1}$ during both study

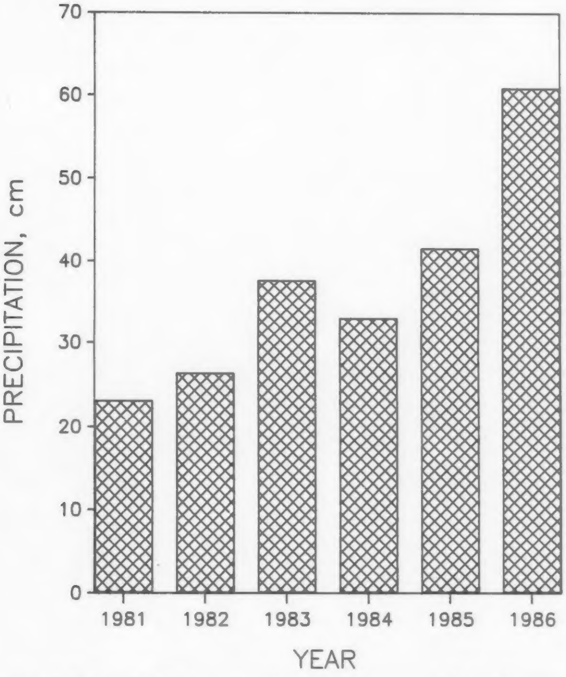

FIG. 1. Total precipitation occurring during the summer "growing season" (1 June to 1 October) in Eau Galle Reservoir between 1981 and 1986. (data collected on site by the U.S. Army Corps of Engineers, St. Paul District Office).

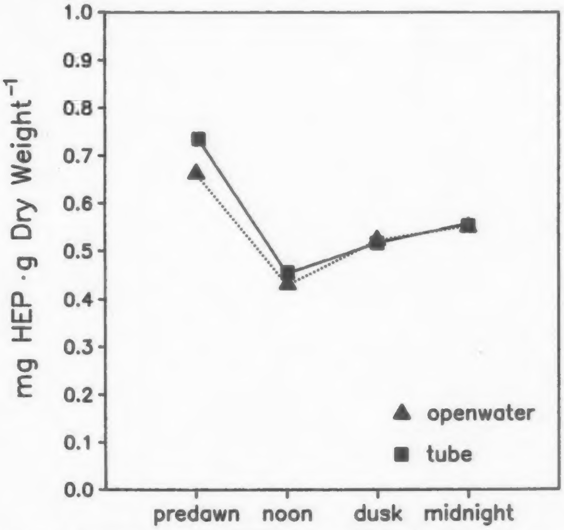

FIG. 2. Concentrations of hot water extractable phosphorus per unit dry weight phytoplankton from depth of peak chlorophyll fluorescence in Eau Galle Reservoir on 7–8 August 1986.

periods; however, differences in SRP loadings were principally a function of hydraulic load.

There were only minor differences in HEP concentrations between the open water and the tube, indicating nutritional similarity between phytoplankton under both sets of conditions (Fig. 2). HEP concentration was less than 0.8 mg·g phytoplankton dry wt^{-1}, indicating potential phosphorus limitation during all times of the day (Fitzgerald and Nelson 1966). Cells had the greatest HEP at dawn and the least at noon. Nocturnal accumulation of phosphorus suggests lower physiological demands and/or greater phosphorus uptake at that time. During this and the previous study period, concentrations of SRP over 0–3 m were less than detection (<0.005 mg·L^{-1}), indicating very effective removal of phosphorus from the epilimnion of Eau Galle. However, there was a gradient below 3 m with ever-increasing concentrations up to a maximum of 0.30 mg·L^{-1} measured just above the sediment surface at 9 m.

Diel migration patterns — *Ceratium* migrated within a water column stratified with respect to both temperature and oxygen concentration during both studies. During the first study, a relatively strong thermal gradient was in effect, and the system was anoxic below about 2 m (Fig. 3). During the second study, thermal stratification was generally less pronounced than during the first, and the depth of anoxia varied between 2 and 3 m (Fig. 4). Transparency was minimal (Secchi ≈ 0.8 m) during both studies due primarily to high algal biomass (an integral average of about 50 μg Chl *a*·L^{-1}) within the 0–3 m stratum. *Ceratium* accounted for 70–80% of the total phytoplankton biomass (about 20 g·m^{-3} as fresh weight) during these studies.

Two distinct migrational patterns were observed. During the first study, *Ceratium* migrated in a manner consistent with that reported frequently in the literature for stationary phase summer populations (Heaney and Furnass 1980; Frempong 1984). The cells concentrated towards the surface during daylight hours and moved downward through the oxycline during the night, but avoided anoxic water below about 2 m (Fig. 5). A slightly asynchronous pattern of ascent and descent was apparent (i.e. ascent started before dawn and descent began prior tc darkness). Oxygen concentration increased from 22.3 mg·L^{-1} (272% saturation) in the morning (10:15) to more than 27 mg·L^{-1} (335% saturation) in the open water by midday (14:00) (Fig. 3). In the second study, *Ceratium* again migrated from near the surface during the late afternoon towards the anoxic zone, but in this case remained broadly dispersed vertically throughout the following day (Fig. 5). Before the end of the day the cells had penetrated to nearly 3 m in both the tube and the open water.

Coincident with the penetration of *Ceratium* cells to 3 m on 8 August was an increase in oxygen concentration to that depth (Fig. 4). This occurred inside the tube as well as in the open water. Weak thermal gradients over 0–3 m during this period facilitated vertical mixing from slight morning breezes. Over an 8-h period, between predawn (05:00) and midday (13:00), there was an integral mean increase in oxygen of 1.45 and 3.8 mg·L^{-1} in the tube and open water, respectively, throughout the 3-m interval.

This net increase in oxygen eliminated the possibility of simple redistribution downward of oxygenated surface water. Sources of oxygen gain in the water column over 0–3 m depth observed in the second study potentially included atmospheric input, lateral transport of oxygen-bearing water from elsewhere, and phytoplankton photosynthesis. Since the surface water was supersaturated with oxygen (123–237%) at that time, the atmosphere could not have served as a source for oxygen. Lateral inputs of dissolved oxygen were clearly precluded within the confines of the tube; however, such contributions could have promoted oxygen increase in the open water. Elevated oxygen

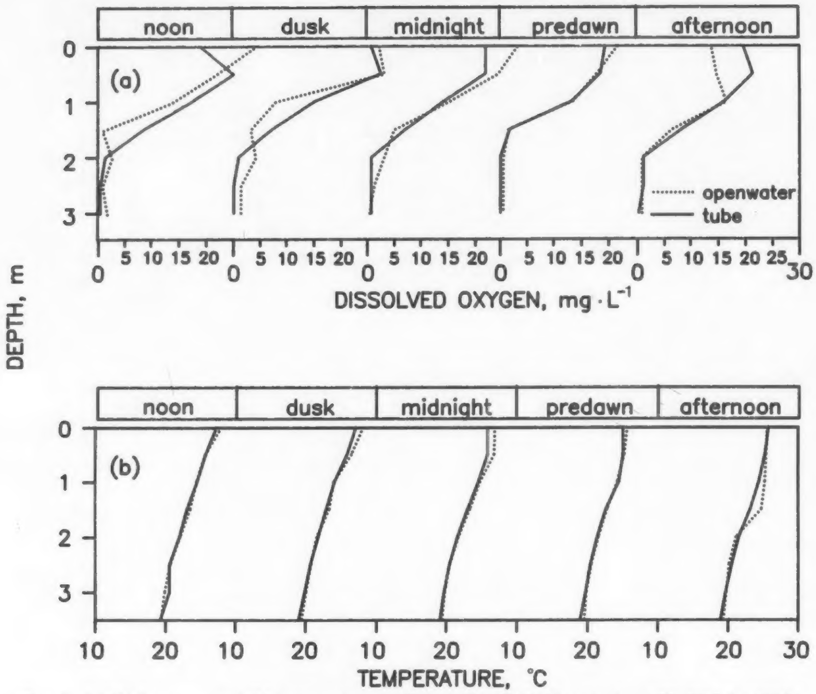

FIG. 3. (a) Diel oxygen and (b) temperature profiles in Eau Galle Reservoir on 29–30 July 1986.

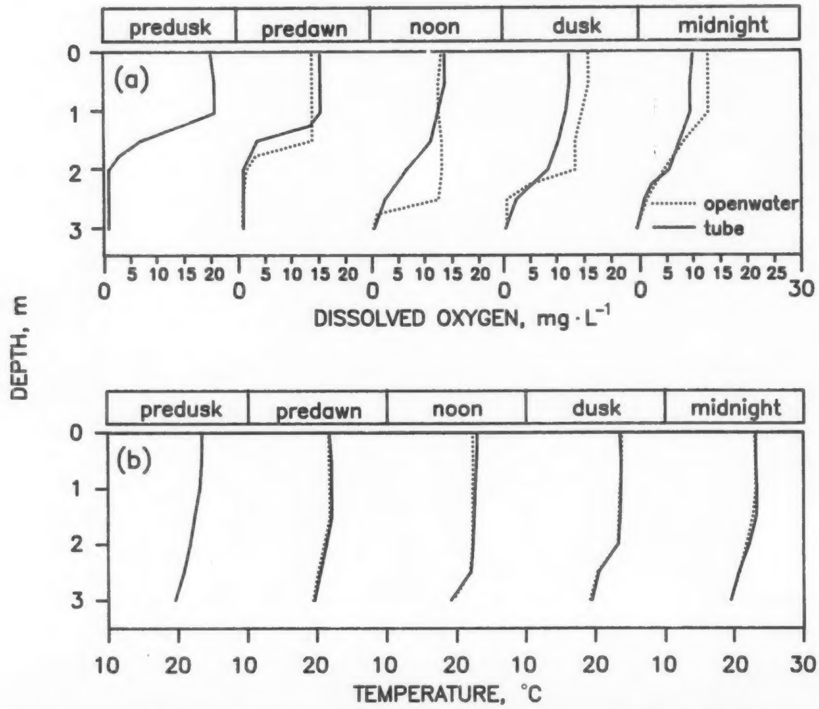

FIG. 4. (a) Diel oxygen and (b) temperature profiles in Eau Galle Reservoir on 7–8 August 1986.

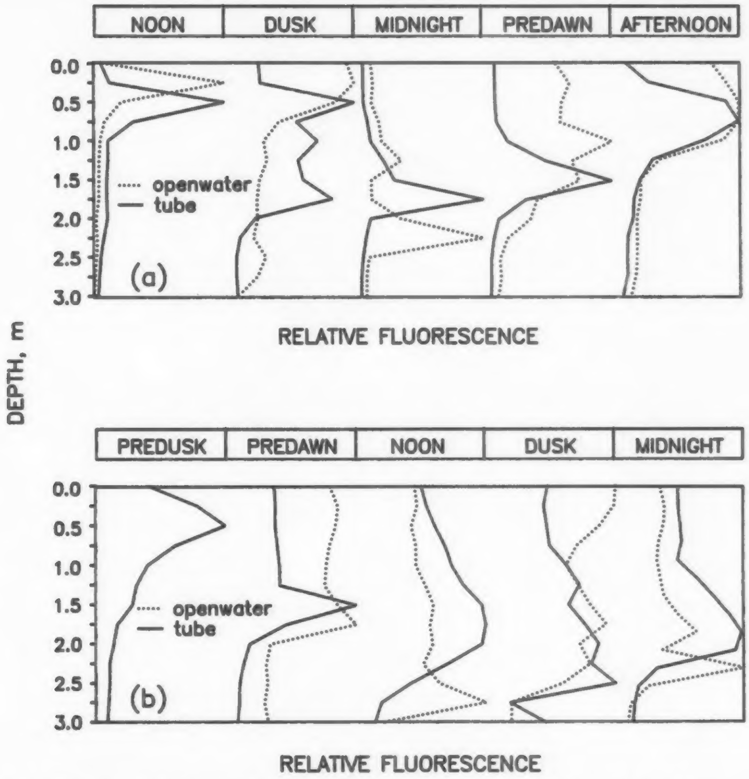

FIG. 5. Profiles of relative chlorophyll fluorescence during (a) 29–30 July and (b) 7–8 August 1986 in Eau Galle Reservoir.

concentrations in both the enclosure and open water were most likely due to phytoplankton photosynthesis.

Interrelationships between nutrition and migration — The impact of watershed nutrients on the phytoplankton community depends on their fate within the reservoir. Past dye studies have indicated that Eau Galle River water traverses the reservoir as interflows in strata of equal density based on temperature. Greatly modified water column chemistry in reservoirs due to riverine interflows has been documented (Nix 1981). In Eau Galle Reservoir, riverine interflows during the summer typically provide nutrient inputs at depths between 2 and 4 m. Given nutrient inputs from storm-related pulses entering the lower epilimnion via these interflows, diel migration by *Ceratium* potentially increases their access to nutrients. Under postulated nutrient (phosphorus) limitation in the second study, cessation of positive phototaxis on the part of *Ceratium* may have increased time of exposure to the relatively more nutritious waters at depth. Nutrient limitation (nitrogen) has been implicated in the cessation of vertical migration in at least one marine dinoflagellate (Eppley et al. 1968). Oxygen production near the oxic–anoxic interface, as observed here, appears to increase the depth to which *Ceratium* can migrate, and hence may potentially further increase nutrient supply.

Periodic pulses of interflowing riverine water at depths proximal to the oxygenated epilimnion increase the chances for interception of phosphorus and other nutrients by *Ceratium*, with subsequent maintenance of the population. Knowledge of interactions among interflow pulsing, associated nutrient loadings, and patterns of vertical migration in *Ceratium* will be necessary to better understand the dynamics of this species in reservoirs. Extensive investigation of these processes with particular attention to phosphorus as a limiting nutrient is continuing at Eau Galle Reservoir.

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Pressions sélectives et nouveautés évolutives : une hypothèse pour comprendre certains aspects des fluctuations à long terme des poissons pélagiques côtiers

Philippe Cury

Chercheur ORSTOM, Institut sénégalais de recherches agricoles, Centre de recherches océanographiques de Dakar-Thiaroye, B.P. 2241, Dakar, Sénégal

Cury, P. 1988. Pressions sélectives et nouveautés évolutives : une hypothèse pour comprendre certains aspects des fluctuations à long terme des poissons pélagiques côtiers. Can. J. Fish. Aquat. Sci. 45: 1099–1107.

L'extinction de certains stocks pélagiques côtiers marins durant des périodes dépassant très largement la durée du cycle de vie des espèces, suivie parfois d'une réapparition brutale et en grande abondance de l'espèce, est observée. Les exemples de la sardine du Japon (*Sardinops melanosticta*), de la sardine du Pacifique (*Sardinops sagax*) et de l'anchois du Pérou et du Chili (*Engraulis ringens*) sont présentés et l'interprétation des fluctuations d'abondance qui en a été faite est rappelée. L'action du climat ou de la pêche n'apparaît pas toujours satisfaisante pour expliquer les processus de récupération de ces stocks. Les travaux menés en écologies marine et terrestre ainsi qu'en biologie évolutive permettent de mieux comprendre les raisons biologiques du maintien et de la récupération des biomasses amoindries. La sévérité de la compétition interspécifique pour l'espèce qui connaît un faible niveau d'abondance est rappelée. Les conséquences possibles de fortes pressions sélectives sur la dynamique des populations ainsi que le fort potentiel adaptatif des espèces pélagiques sont soulignées. Enfin, l'aptitude d'une espèce à exprimer une nouveauté évolutive lorsqu'elle est devenue rare dans le milieu est envisagée. Ainsi, nous émettons comme hypothèse que les longues périodes d'extinction au caractère attractif sont le fruit de pressions sélectives fortes et du moindre impact des fluctuations climatiques. La reconstitution de biomasses qui se sont éteintes mettrait en jeu un processus adaptatif (microévolution) qui permettrait de sortir de l'état attractif que constituent les faibles biomasses. La sélection naturelle pourrait ainsi se mêler aux mécanismes de régulation des populations pélagiques. Un modèle de type théorie des catastrophes est proposé pour illustrer la régulation à long terme de ces systèmes pélagiques.

The extinction during periods much longer than the duration of a species life cycle followed by a quick resurgence to high abundance levels is sometimes observed in marine coastal pelagic stocks. Japanese sardine (*Sardinops melanosticta*), Pacific sardine (*Sardinops sagax*), and Peruvian and Chilian anchovy (*Engraulis ringens*) are presented as examples. Interpretations of these stocks' fluctuations are reviewed. Climatic events and the influence of commercial harvesting do not always appear sufficient to explain such recoveries. Approaches derived from marine and terrestrial ecology as well as from evolutionary biology may lead to a better understanding of the biological reasons for the maintenance and recovery of depleted biomasses. The importance of interspecific competition during periods of low biomass levels is discussed. The possible consequences of strong selective pressures on population dynamics and the adaptive potential of pelagic species are emphasized. Lastly, evolutionary novelties that appear when a species is becoming depleted are considered. From these considerations, we hypothesize that the long attractive periods of low abundance can result from strong selective pressures and from the reduced influence of climatic events. The recovery of depleted biomasses would be the result of an adaptive process (microevolution). Natural selection could therefore act as another regulation mechanism for marine pelagic populations. A model using catastrophe theory is proposed to ilustrate the long-term regulation of these pelagic systems.

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Dans les écosystèmes côtiers, le nombre des espèces de poissons pélagiques est toujours faible et dépasse rarement la dizaine alors que les zones démersales sont colonisées par plusieurs dizaines, voire plus d'une centaine d'espèces. Un certain nombre d'écologistes et de biologistes de l'évolution se sont interrogés sur cette faible diversité : pourquoi n'y a-t-il pas plus d'espèces de poissons pélagiques ? Pour MacArthur (1975), Sanders (1968), Mayr (1981) et Colinvaux

(1982) peu d'espèces sont capables de s'adapter à un environnement aussi peu prédictible que le milieu pélagique. Les espèces pélagiques côtières ont en effet colonisé les zones d'upwelling ou de fronts dont une des caractéristiques essentielles est leur très grande variabilité spatiale et temporelle. Outre le faible nombre d'espèces de poissons, l'instabilité des stocks, voire le changement de composition spécifique, apparaît aussi comme une caractéristique importante des écosystèmes pélagiques (Kawai et Isibasi 1983). Les pays concernés par l'exploitation de ces espèces savent bien que les effondrements de stocks sont courants et douloureux pour leur économie puisqu'il n'y a souvent pas d'espèces susceptibles de remplacer celles qui ont disparu de la pêcherie (Troadec *et al.* 1980). Aussi, une attention toute particulière est portée par la communauté scientifique internationale au suivi de ces stocks qui sont devenus les espèces d'animaux sauvages abondants parmi les mieux étudiées (Cushing 1982).

Si, lors des phases d'effondrement des stocks, les théories sont nombreuses et les exemples bien documentés, la documentation reste beaucoup plus discrète sur leur comportement durant les phases de faible abondance et sur les mécanismes de recouvrement des biomasses. Les poissons marins pélagiques côtiers qui ont connu un effondrement ont cette impressionnante faculté de réapparaître après des périodes de temps très variables. Il faut reconnaître qu'aucune analyse scientifique ne permet à l'heure actuelle de savoir, même avec une grande imprécision, quand et à quel niveau de biomasse un stock se reconstituera (Shannon *et al.* 1984).

Nous proposons d'analyser les plus connus de ces exemples d'effondrement de stocks en focalisant notre attention sur les périodes de recouvrement. Nous donnerons ensuite les raisons qui nous amènent à formuler des hypothèses nouvelles sur les mécanismes qui sont peut-être mis en jeu lors de la récupération de ces stocks en considérant une approche relevant de la biologie évolutive.

L'extinction temporaire des stocks : un phénomène naturel ?

Nous présenterons trois exemples extrêmement connus pour leur importance économique et qui ont été étudiés sur une longue période de temps : celui de la sardine du Japon (*Sardinops melanosticta*), celui de la sardine du Pacifique (*Sardinops sagax*) et celui de l'anchois du Pérou et du Chili (*Engraulis ringens*). Nous décrirons succintement les fluctuations d'abondance de ces stocks ainsi que les interprétations qui en ont été données.

Les faits et les interprétations

La sardine du Japon

La sardine du Japon vit et se reproduit dans les eaux côtières limitées par deux courants chauds, le Kuroshio des eaux du Pacifique et le Tsushima de la mer du Japon et de l'est de la mer de Chine. L'identification du nombre de stocks de sardines a fait l'objet de nombreux débats qui restent ouverts (Nakai 1962; Uda 1952). Cependant d'après les observations les plus récentes (Kondô 1980), le stock de sardines serait constitué de quatre races ou sous-populations distribuées et se reproduisant dans des zones géographiques différentes situées autour du Japon. Ces différentes sous-populations ont été exploitées intensivement durant la période 1930–1940 (fig. 1). Les débarquements atteignirent plus de 2,5 millions de tonnes (fig. 1). Après un effondrement spectaculaire qui eut lieu dans les années 1941–1943, les stocks furent réduits durant plus de 27 années à un niveau très bas puisque les captures ne dépassèrent jamais 0,4 million de tonnes (fig. 1). La sardine avait disparu des côtes japonaises (Kondô 1980). Après cette phase extrêmement longue d'absence dans la pêcherie, une récupération rapide et soutenue de la sous-population du Pacifique eut lieu à partir de 1973 (fig. 1). En 1984 on pêchait environ 4 millions de tonnes de sardines autour du Japon, c'est-à-dire presque deux fois plus que durant la période de grande abondance précédente. Cette rapidité et cette intensité du recouvrement étaient dues à une succession de très bons recrutements dans la pêcherie (fig. 1).

Ces périodes de prospérité suivies d'une extinction quasi totale de la population de sardine semblent faire partie de l'histoire naturelle de ces populations. À partir des faits relatés dans la documentation ancienne concernant l'activité des pêcheries, Tsuboi (1984) a pu mettre en évidence environ six périodes durant lesquelles cette espèce a été abondante depuis le XVII^e^ siècle. Les durées des périodes de faible abondance sont très variables puisqu'elles sont apparemment comprises entre 20 et 100 ans.

L'interprétation de l'effondrement de ces stocks ainsi que leur récupération pendant la période récente ont fait l'objet de controverses. Pour Cushing (1971), le déclin important du recrutement observé dans les années quarante résulte d'une pêche trop intense. Si personne ne conteste l'accélération probable de l'effondrement du stock dû à la pêche, pour la plupart des auteurs son impact sur la dynamique de ce stock paraît mineur comparé à celui de l'action des fluctuations climatiques. Nakai (1949, 1962) et Kondô (1980) insistent sur l'importance de la nature des ondulations du courant chaud du Kuroshio. Ce courant connaît des oscillations près de la côte plus ou moins prononcées par rapport à un type de circulation générale. Ces fluctuations auraient un effet significatif sur la production d'oeufs (Watanabe 1981) et l'alimentation des larves (Kondô 1980) et par conséquent sur le recrutement et les captures totales (Watanabe 1983). Sur la figure 1 est portée la durée des ondulations de fortes (lettre A) ou de moyennes amplitudes (lettres B et C) du Kuroshio, indiquant la persistance des eaux froides plaquées à la côte. Yamanaka (1984) montre que la diminution des captures en 1941 et en 1957–1958 correspond à des années d'apparition à grande échelle du phénomène d'El Niño (fig. 1). Outre ces hypothèses faisant intervenir l'action climatique sur des phases sensibles du cycle de vie des espèces, deux autres types d'arguments ont été avancés. L'importance possible de la compétition avec le stock de maquereau *Scomber japonicus* a été souligné (Kawai et Isibasi 1983; Tanaka 1983). Watanabe (1981) et Hayasi (1983) ont mis l'accent sur une modification profonde des stratégies de migrations de l'espèce durant la phase de prospérité du stock avec l'apparition d'un groupe de poissons doué de facultés de migrations de grandes amplitudes.

La figure 1 synthétise l'évolution d'un certain nombre de facteurs climatiques qui sont apparus comme étant importants pour la dynamique de ce stock. Elle souligne le fait que si certains facteurs climatiques-clefs concordent avec les phases d'extinction ou de prospérité du stock, ceux-ci n'apportent pas toujours les réponses souhaitées pour comprendre l'évolution de ces stocks sur l'ensemble de la période considérée (Kawai et Isibasi 1983).

La sardine du Pacifique

Les années trente et quarante furent prospères pour les pêcheries côtières californiennes avec des débarquements annuels

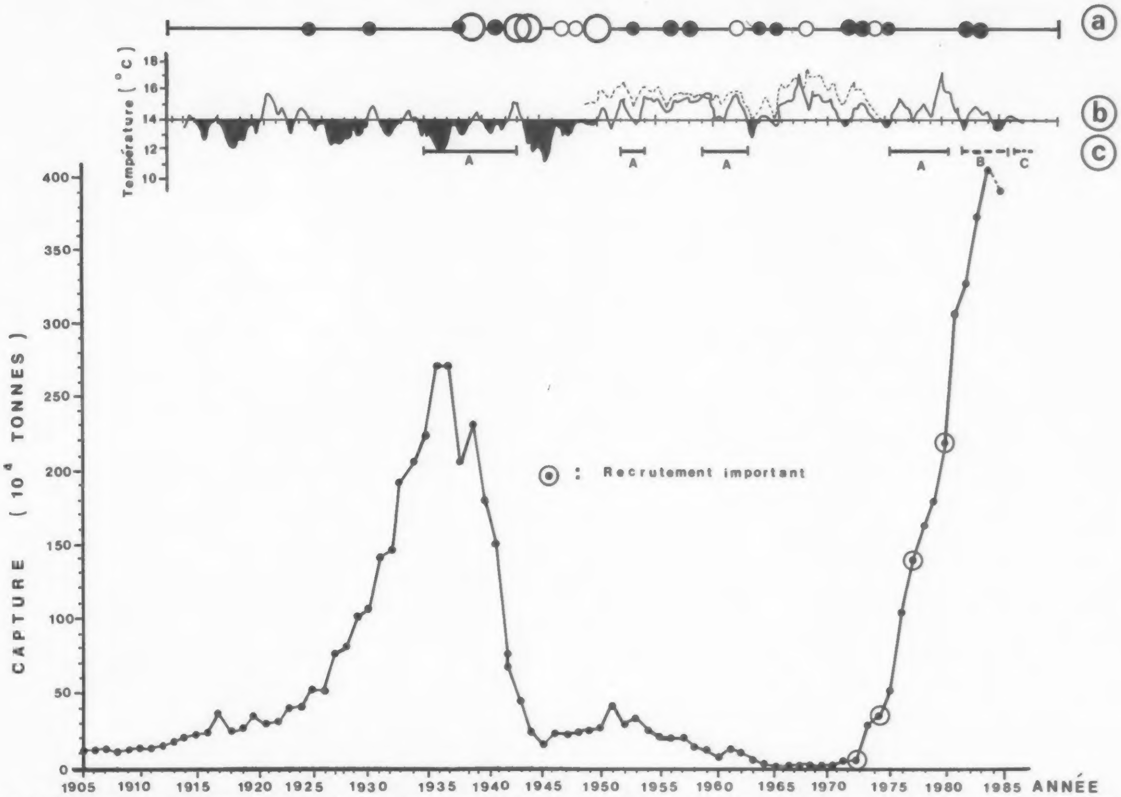

FIG. 1. Fluctuations climatiques et pêche de la sardine autour du Japon entre 1905 et 1985 (d'après Watanabe 1981 et Kondô 1987): a) index El Niño (d'après Yamanaka 1984) : (●) fort, (•) moyen, (◯) faible, (○) très faible; b) températures côtières mesurées sur la face du Pacifique du Japon (d'après Kondô 1987); c) méandres du Kuroshio (d'après Kondô 1987; voir texte).

compris entre 500 000 et 700 000 tonnes (Marr 1960). Au début des années cinquante le stock de sardine s'effondre et les captures deviennent insignifiantes dans les différents ports situés tout au long de la côte (fig. 2). Malgré une brève réapparition en 1958, la sardine disparaît complètement des côtes californiennes et depuis cette date une interdiction totale frappe la pêche de cette espèce. Des campagnes océanographiques exploratoires menées en 1982 (Mais 1982) laissent entrevoir la possibilité d'une récupération prochaine du stock (MacCall 1983).

Les analyses démographiques indiquaient une surexploitation de cette population (Murphy 1966). Récemment MacCall (1983) a suggéré que l'effondrement de ce stock était dû à un taux d'exploitation qui a toujours été trop élevé entre 1930 et 1960. L'hypothèse de l'influence de variations climatiques défavorables durant une longue période ne peut être écartée (Troadec *et al.* 1980). Ainsi Lasker et MacCall (1983) s'étonnent que le stock de sardines ait mis environ 15 ans pour récupérer du bas niveau de biomasse des années 1870, alors qu'il y a plus de 30 ans que la sardine a disparu des eaux californiennes. Un argument a été avancé par MacCall (1979) pour tenter de comprendre l'absence de fluctuations d'abondance de ce stock depuis 1960. Cet auteur note que les très faibles recrutements observés dans les années 1960 sont vraisemblablement le résultat de poissons qui ont migré depuis le sud et qui sont génétiquement moins bien adaptés pour pondre dans les eaux froides devant la Californie.

L'histoire des fluctuations d'abondance des populations de poissons pélagiques a pu être reconstruite dans cette zone grâce aux travaux paléoécologiques de Soutar et Isaacs (1969, 1974). Grâce à une étude des dépôts d'écailles dans les sédiments anaérobies, ces auteurs ont pu établir une série chronologique sur près de 2 000 ans des fluctuations apparentes des biomasses de la sardine du Pacifique (Soutar et Isaacs 1969). Pour la période récente des 200 dernières années, il apparaît des variations extrêmement importantes des biomasses avec des déclins ou des récupérations de stocks rapides en dehors de toute pêcherie (Soutar et Isaacs 1974). Ces fluctuations à long terme indiquent que la sardine a été aussi souvent absente que présente (Troadec *et al.* 1980).

L'anchois du Pérou et du Chili

La pêcherie d'anchois de l'upwelling péruvien a été la plus importante pêcherie du monde. Après une croissance rapide de son activité à partir des années soixante, la flottille débarquait durant la période allant de 1965 à 1971 entre 7,2 et 12,3 millions de tonnes (fig. 3B). Un effondrement du stock eut lieu en 1972–1973 et depuis les captures ne dépassent pas 4 millions de tonnes (fig. 3B). Bien qu'étant un stock de moindre importance, l'anchois pêché sur les côtes chiliennes a suivi la même destinée. Les captures avoisinaient le million de tonnes entre

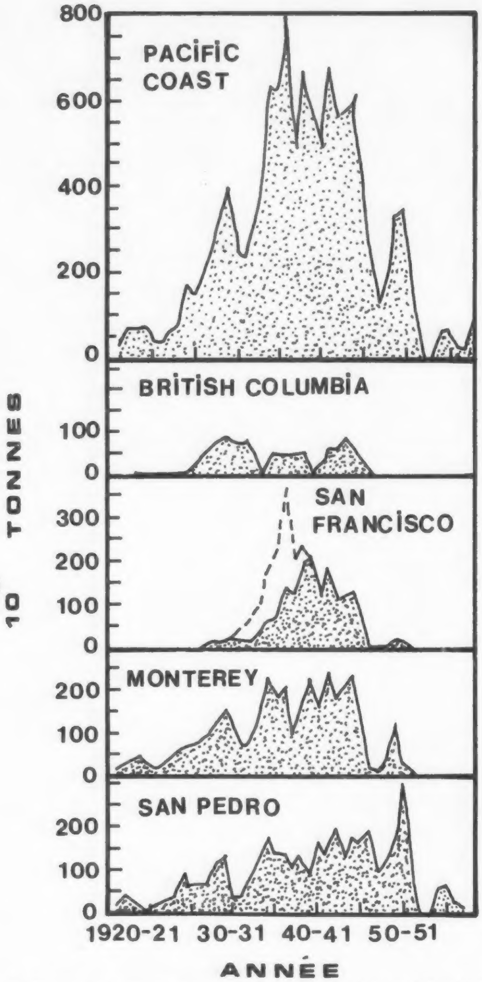

FIG. 2. Captures de sardines sur la côte nord-américaine (d'après Marr 1960).

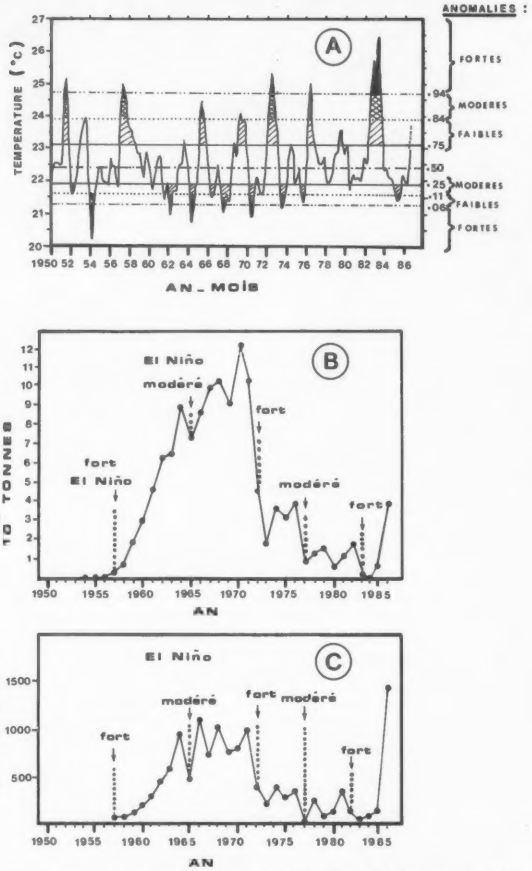

FIG. 3. Fluctuations climatiques et pêche de l'anchois le long des côtes péruviennes et chiliennes entre 1950 et 1986: A) températures de surfaces lissées et ajustées entre 0°–10° S et 90°–80° W (d'après Flueck et Brown 1987); B) captures d'anchois au Pérou (d'après Zuta *et al.* 1983; Annuaires statistiques FAO); C) captures d'anchois au Chili (d'après Jordan 1983; Yañez *et al.* 1986; Annuaires statistiques FAO).

1966 et 1971; après 1972, elles ne dépassent jamais 0,5 millions de tonnes (fig. 3C). Un accroissement brutal des captures a eu lieu au Chili et dans une moindre mesure au Pérou en 1986.

L'action d'El Niño, un courant chaud d'origine transocéanique qui apparaît irrégulièrement le long des côtes péruviennes et chiliennes, paraît déterminante sur la dynamique de ce stocks (Cushing 1982; Jordan 1983; Zuta *et al.* 1983; Serra 1987). L'apparition périodique d'El Niño affecte la productivité des eaux d'upwelling des côtes péruviennes et chiliennes (fig. 3). Pour Cushing (1982) il fallait cesser toute pêche de cette espèce pour que le stock ait une chance de se reconstituer. Bien que l'exploitation se soit poursuivie, l'anchois semble à nouveau abondant au Chili et au Pérou depuis 1986.

L'interprétation des structures sédimentaires et la datation à l'aide du carbone 14 ont permis à De Vries et Pearcy (1982) de montrer que les biomasses d'anchois du Pérou ont grandement fluctué depuis 16 000 ans. Cette espèce a connu, tout comme les sardines du Japon ou du Pacifique, des périodes de prospérité suivies de périodes d'absence dans le milieu.

Conclusion

Les exemples de fluctuations d'abondance d'espèces pélagiques côtières sont nombreux (Shannon *et al.* 1984). Nous avons résumé ceux qui nous semblaient les mieux documentés. Ces exemples nous renseignent sur la dynamique de ces espèces et sans prétendre à une généralisation, plusieurs remarques importantes peuvent être faites. Tout d'abord la dynamique de ces ressources pélagiques apparaît comme instable et imprévisible : ces stocks connaissent des phases de prospérité suivies de périodes d'extinction quasi totales. Si les effondrements sont fréquents, les recouvrements le sont aussi (Lasker et MacCall 1983). Ce phénomène semble faire partie de l'histoire naturelle de ces espèces comme en témoignent les récentes recherches en paléoécologie, bien qu'il apparaisse que l'effondrement de stocks soit accentué par une pêche trop intense. Un autre point important est qu'il ne semble pas y avoir de niveau minimum des stocks pour lequel le recouvrement soit impossible (Lasker 1985). Il apparaît aussi que les périodes durant lesquelles les stocks sont éteints sont souvent largement supérieures à la durée du cycle de vie des espèces. Pour la sardine du Japon, la sardine

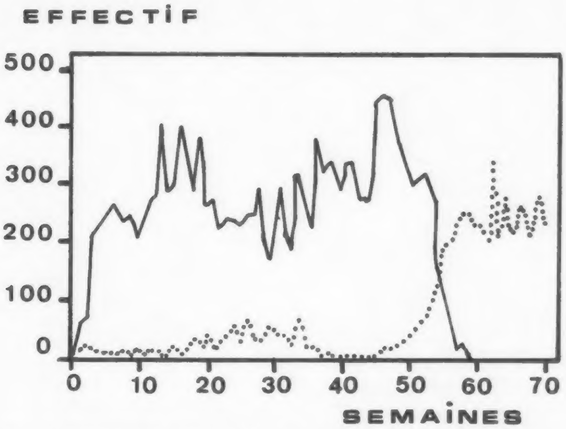

FIG. 4. Dynamique de l'évolution de deux populations compétitrices de mouches (*Musca domestica* et *Phaenicia sericata*). Le renversement de dominance qui s'établit après 45–50 semaines traduit l'intervention d'un processus sélectif (d'après Pimentel *et al.* 1965).

du Pacifique et l'anchois du Pérou et du Chili, les phases d'extinction observées durant les périodes récentes ont duré respectivement 29 ans, plus de 30 ans et plus de 13 ans, alors que ces espèces ne vivent que 6, 8 et 4 ans. Les mécanismes de récupération des stocks ne sont pas progressifs et tout se passe comme si les faibles abondances observées durant les périodes d'extinction étaient des états attractifs, les biomasses des stocks amoindries fluctuant alors très peu.

Discussion : le besoin de nouvelles hypothèses ?

Pour les biologistes, la raison d'être de longues périodes d'extinction suivies de rapides récupérations de stocks soulève des problèmes : pourquoi ces stocks restent-ils éteints durant de longues périodes et pourquoi se reconstituent-ils parfois très rapidement ? Deux facteurs ont été identifiés comme pouvant jouer conjointement ou non un rôle important pour comprendre la dynamique de ces systèmes : l'effet de la variabilité du recrutement et celui de la compétition interspécifique. Ces deux facteurs ne sont d'ailleurs sûrement pas indépendants pour les stades pré-recrues; la compétition est en effet l'un des nombreux phénomènes invoqués comme pouvant influencer le recrutement (Lasker 1985). Il est classiquement admis que la variabilité climatique joue un rôle important sur le recrutement de ces espèces (Blaxter et Hunter 1982). Durant les longues périodes d'extinction, les biomasses amoindries ont vraisemblablement subi des conditions climatiques qui leur étaient parfois favorables; cependant il n'y a pas eu de reconstitutions des stocks éteints. L'étude des fluctuations climatiques appréhendées par certains paramètres précis ou les quelques éléments disponibles relatifs aux espèces compétitrices n'ont pas apporté d'interprétation satisfaisante. Il n'y a pas d'indices climatiques ou biologiques qui, pris individuellement, peuvent apporter une réponse claire à ces interrogations. La question reste donc en suspens : comment un niveau de biomasse très faible peut-il être maintenu durant une longue période et quels sont les mécanismes qui peuvent induire un recrutement important à un bas niveau du stock ?

Devant les difficultés que présentait l'interprétation des fluctuations des ressources pélagiques, plusieurs auteurs (Kawasaki 1983; Shannon *et al.* 1984) ont tenté de comparer la dynamique d'un certain nombre de stocks dans différentes zones. Constatant des fluctuations synchrones de certains stocks, ils ont tenté de trouver des facteurs explicatifs communs. Dans l'état actuel des connaissances, il demeure difficile d'identifier des grands cycles climatiques mondiaux susceptibles d'affecter la dynamique à long terme de ces stocks. De plus, une sérieuse limitation existe à ce type d'approche car les variations d'abondance des espèces vivant dans un même ecosystème sont généralement d'amplitudes et de fréquences indépendantes (Troadec *et al.* 1980). En effet il apparaît raisonnable de penser que, les stratégies de vie de ces espèces étant différentes, les facteurs responsables des fluctuations d'abondance le sont aussi.

Les mécanismes qui entretiennent les périodes d'extinction ainsi que ceux qui permettent à des stocks de recouvrer une certaine prospérité ont besoin d'être mieux compris. La dynamique de ces stocks de petits poissons pélagiques n'est vraisemblablement pas régie par un mécanisme simple mais par un ensemble de mécanismes subtils et agissant de façon différente selon le niveau d'abondance du stock. Dans le paragraphe qui suit nous proposons de discuter la dynamique de ces stocks en reprenant certains arguments avancés en biologie évolutive.

Pressions sélectives et nouveautés évolutives : une hypothèse pour interpréter le recouvrement de certains stocks

Sévérité de la compétition interspécifique pour les bas niveaux des stocks et ses implications

Haldane (1932) soulignait que lorsque deux espèces sont en compétition et que l'une devient rare, elles subissent des pressions sélectives dissymétriques : l'espèce dominée a des contacts interspécifiques alors que l'espèce abondante a des contacts essentiellement intraspécifiques. On peut ainsi penser que la réaction des stocks est différente selon le niveau relatif de leur abondance. Lorsque le stock est prospère, les contacts sont principalement intraspécifiques et la pression sélective due à la compétition est lâche; lorsque le stock est très réduit, les contacts sont interspécifiques et la pression sélective forte.

Il est particulièrement difficile de relever et mettre en évidence de telles subtilités dans le milieu marin et il faut nous reporter aux travaux expérimentaux terrestres de Moore (1952) ou de Pimentel *et al.* (1965) pour connaître les implications de tels phénomènes au niveau des populations. Ces auteurs ont réuni dans un même milieu deux espèces compétitrices de mouches dont une compétitivement supérieure, devenue par conséquent beaucoup plus abondante en début d'expérience (fig. 4). Au bout d'un certain temps, se produit un renversement de dominance compétitive qui aboutit à l'extinction de l'espèce la plus abondante (fig. 4). D'après ces auteurs, un tel renversement d'équilibre traduit l'intervention d'un processus sélectif et confirme la réalité d'une microévolution. Il y aurait donc eu une modification qualitative de la population dominée, ce qui lui aurait permis de devenir à son tour compétitivement supérieure. Ces modifications ou nouveautés évolutives peuvent être considérées comme étant « n'importe quelle structure ou propriété nouvellement acquise qui permet d'assurer une nouvelle fonction, laquelle, à son tour, ouvrira une nouvelle zone adaptative » (Mayr 1974). Des changements de comportement, même subtils, peuvent en effet avoir des conséquences importantes sur la survie des individus et peuvent permettre l'expansion d'une population (Mayr 1981).

Les biomasses des stocks de certaines espèces pélagiques se sont développées après l'effondrement de la sardine du Japon,

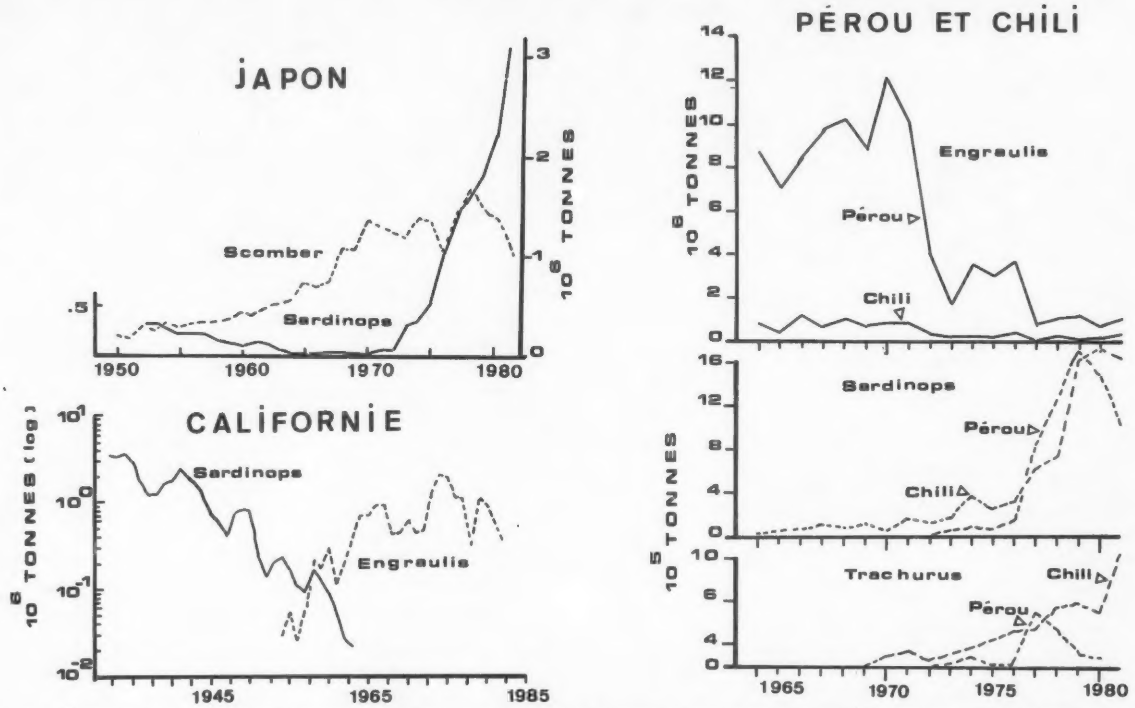

FIG. 5. Évolution des captures (ou biomasses) de sardines et de l'anchois (ligne continue) ainsi que celle des espèces compétitrices associées (ligne brisée) au Japon (d'après Tanaka 1983), en Californie (d'après MacCall 1986) et au Pérou et au Chili (d'après Jordan 1983).

de la sardine du Pacifique et de l'anchois du Pérou et du Chili : il s'agit respectivement du maquereau (*Scomber japonicus*) (Tanaka 1983), de l'anchois (*Engraulis mordax*) (Lasker et MacCall 1983), et de la sardine (*Sardinops sagax*) et du chinchard (*Trachurus murphyi*) (Jordan 1983; Yañez *et al.* 1986). Si l'interprétation de ces exemples, présentés sur la figure 5, est sujet à de nombreuses controverses, la compétition interspécifique demeure une hypothèse importante généralement retenue lorsque l'on aborde l'étude de ces écosystèmes pélagiques. La sévérité de la compétition interspécifique pour les bas niveaux de stocks est par conséquent vraisemblable. Mais les espèces pélagiques côtières sont-elles aptes à présenter de telles nouveautés au sein de leur population; en d'autres termes possèdent-elles un fort potentiel adaptatif ?

Potentiel adaptatif des espèces pélagiques côtières

Deux caractéristiques essentielles peuvent conférer aux populations de poissons pélagiques un fort potentiel adaptatif : le potentiel biotique et la plasticité démographique.

Les espèces pélagiques possèdent des potentiels biotiques importants; chaque femelle peut pondre plusieurs milliers ou millions d'oeufs et ceci plusieurs fois durant l'année alors que le renouvellement de la population nécessite la survie de seulement deux individus. La disponibilité d'une grande quantité de variation génétique non utilisée à chaque génération représente un grand avantage sélectif (Mayr 1981). En effet, le taux d'évolution d'une population est directement lié au taux de variation génétique présent dans la population (Ayala 1977). Les environnements physique et biologique fluctuent beaucoup dans le milieu pélagique, il est donc impossible de prédire la combinaison particulière de gènes qui sera la plus avantageuse dans la génération suivante. Dans ces circonstances, la probabilité est alors élevée que certains génotypes soient optimaux dans des circonstances nouvelles (Mayr 1981). Ainsi, ces espèces seraient capables de subir un ajustement rapide au changement de l'environnement ou d'adopter un nouveau mode de vie, sous certaines conditions que nous préciserons dans le paragraphe suivant.

La plasticité d'un caractère, c'est-à-dire sa variance et non pas sa valeur moyenne, est aussi une réponse adaptative très importante (Levins 1968; Barbault et Blandin 1980). Certains paramètres démographiques des espèces pélagiques étudiées présentent une remarquable variabilité (facteurs de condition, indices gonado-somatiques, tailles de première reproduction, vitesses de croissance, etc.). Ainsi, les mécanismes adaptatifs pourraient faire intervenir l'évolution d'un caractère ou la canalisation de la variabilité de ce caractère (Stearns 1980). Stearns (1982) définit deux types de plasticité : la plasticité continue et la plasticité discrète. La plasticité continue est définie comme étant la réponse permanente de caractères individuels à des variables environnementales (telles la température, la salinité, etc.); la plasticité discrète, appelée « developmental switches » par Levins (1968), constitue la production d'individus présentant des formes alternatives parfois mieux adaptées et qui peuvent s'exprimer au sein d'une population. La différence entre les deux peut paraître conceptuelle car il n'est pas actuellement possible de comprendre leur incidence respective en biologie évolutive.

Expression de nouveautés évolutives et taille de la population

Un autre facteur essentiel à la compréhension de ces méca-

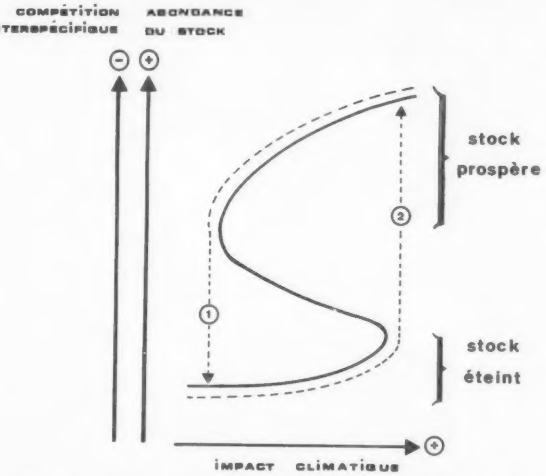

Fig. 6. La régulation à long terme de type « catastrophe » de l'abondance des stocks de poissons pélagiques peut être représentée à l'aide d'un modèle de fronce bidimensionnel tiré de la théorie des catastrophes (voir texte).

nismes évolutifs est la taille de la population. Ces nouveautés évolutives ne peuvent apparaître que dans des populations à faible effectif (voir par exemple Mayr 1960). Une façon intuitive de présenter ce résultat est de considérer que lorsqu'un regroupement de gènes est très grand, la fixation et la conservation d'une nouveauté évolutive sont rendues difficiles du fait de sa dilution dans la population, et le changement évolutif se fait lentement. L'expression d'une nouveauté évolutive serait donc favorisée par des populations réduites, telles les populations qui se sont effondrées.

Impact de la variabilité climatique et taille de la population

Nous venons de discuter de pressions sélectives et de nouveautés évolutives qui peuvent apparaître chez certaines populations aux effectifs réduits. Les travaux de Skud (1982, 1983) apportent quelques réflexions complémentaires quant au comportement possible de ces populations vis à vis des facteurs climatiques. Cet auteur montre que la réaction du stocks vis-à-vis des facteurs climatiques peut être inversée en cas de dominance. L'abondance de l'espèce étant alors contrôlée par l'abondance de l'espèce dominante, la réponse aux facteurs climatiques apparaît moindre et peut alors changer. Bien que les raisons d'être de telles inversions restent méconnues, Skud (1982, 1983) montre ainsi que le recrutement de la sardine de Californie et la salinité sont positivement corrélés lorsque l'espèce est abondante, alors que ces mêmes variables sont corrélées négativement lorsque l'espèce est devenue rare dans le milieu. La relation entre abondance et température s'inverse également.

Une dynamique des populations qualitative ?

L'ensemble de ces résultats et réflexions montre que la réponse des populations aux pressions sélectives interspécifiques et environnementales diffèrent peut-être selon l'état des stocks. Les populations ayant atteint un bas niveau de biomasse, étant soumises à de fortes pressions sélectives, des nouveautés évolutives peuvent s'exprimer. Ford (1975) a montré que celles-ci peuvent apparaître très rapidement au sein d'une population, rendant l'échelle des processus écologiques et évolutionnistes comparables. La sélection naturelle peut ainsi se mêler aux mécanismes de régulation des populations (Krebs 1978). Nous proposons, en reprenant les arguments qui viennent d'être exposés, d'interpréter les longues périodes d'extinction et leur caractère attractif comme le fruit de pressions sélectives fortes et d'un impact réduit des fluctuations climatiques. Quel que soit le niveau d'abondance du stock effondré, sa reconstitution est possible; des exemples concrets l'ont montré. L'impact du climat sur cette reconstitution, c'est-à-dire sur le succès du recrutement, n'a pas pu être clairement mis en évidence. Ceci nous amène naturellement à penser qu'il pourrait exister une relation nouvelle entre la population et son environnement. Cette reconstitution pourrait être alors le fruit de nouveautés évolutives, c'est-à-dire d'une modification qualitative de la population dans un nouveau contexte de pressions sélectives interspécifiques et environnementales.

Régulation de type « catastrophe » des systèmes pélagiques

La théorie des catastrophes a été proposée afin de modéliser la nature discontinue de certains phénomènes naturels (Thom 1972; Zeeman 1978). Un modèle de fronce bidimensionnel peut permettre de synthétiser et illustrer les hypothèses faites sur la régulation à long terme des systèmes pélagiques (fig. 6). Sur cette figure, la ligne discontinue représente le chemin possible sur la topologie théorique (ligne continue). La sévérité de la compétition interspécifique est fonction de l'abondance du stock; elle est faible (signe −) pour un stock prospère et forte dans le cas d'un stock éteint (axe des Y). Le stock s'effondre quand son niveau est trop bas et dans des conditions climatiques défavorables (chemin 1). Le stock éteint fluctue alors peu, même lorsque les conditions climatiques sont favorables (signe +). Ce stock peut cependant recouvrer un important niveau de biomasse pour des conditions climatiques favorables et lorsque des nouveautés évolutives apparaissent dans un contexte de fortes pressions sélectives (compétition interspécifique) (chemin 2).

Conclusions

Les exemples d'apparitions et de disparitions sporadiques de stocks sont fréquents (Dajoz 1974; Cushing 1982) et les raisons avancées pour expliquer de tels bouleversements sont variées. La récupération des stocks qui ont connu un effondrement n'est vraisemblablement pas régie par des mécanismes simples. Nous ne prétendons donc pas expliciter le mécanisme responsable de ces processus, mais seulement analyser des exemples de récupération de certains stocks pélagiques côtiers (notamment sardines et anchois), en reprenant les concepts développés en biologie évolutive. Cette approche qualitative nous paraît être complémentaire à l'approche classiquement faite pour aborder la dynamique de ces populations. Les voies tracées par les travaux récents sur les adaptations évolutives physiologiques (Eastman et DeVries 1987) paraissent à ce titre prometteuses quant à l'avenir des recherches en biologie évolutive marine.

Si la validité des théories évolutionnistes est difficilement testable, il n'en demeure pas moins qu'elles peuvent cependant contribuer à une perception nouvelle du fonctionnement passé des populations exploitées et de leur avenir (Barbault 1984). L'approche en biologie évolutive apporte une aide à la compréhension de la dynamique des populations, mais elle peut aussi déboucher comme toute science interprétative sur une mythification des observations et une appropriation interprétative des faits comme le souligne Jacob (1981).

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